

Historic, Archive Document

Do not assume content reflects current scientific knowledge, policies, or practices.

Reserve

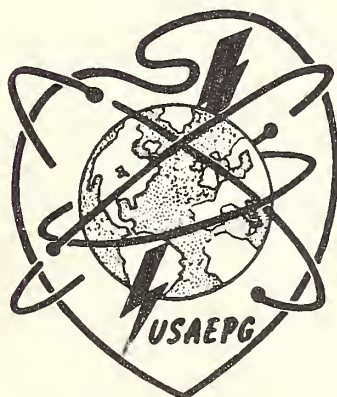
A451
508

PURCHASED BY
AGRICULTURAL LIBRARY

USAEPG 6-42-61

ANNUAL REPORT
RESEARCH IN PLANT TRANSPIRATION

TASK 3A99-27-005-08



U. S. DEPT. OF AGRICULTURE
NATIONAL AGRICULTURAL LIBRARY

MAR 11 1964

C & R-PREP.

U.S. ARMY ELECTRONIC PROVING GROUND
FORT HUACHUCA, ARIZONA
OCTOBER 1961

3
ANNUAL REPORT
OF
RESEARCH IN PLANT TRANSPIRATION

8
DA Task 3A99-27-005-03

by
G. G. Williams, James E. Pallas, Jr.,
Donald G. Harris, and Charles B. Elkins,
Jr.

2a
Southern Piedmont Soil Conservation Field Station, +26
Agricultural Research Service
U.S. Department of Agriculture
2b Watkinsville, Georgia

Under Cross Service Order
USAEPG 3-59

for

7
U.S. Army Electronic Proving Ground,
Fort Huachuca, Arizona
October 1961 +7a (on cover)

THE JOURNAL OF THE

THE JOURNAL OF THE



THE JOURNAL OF THE

THE JOURNAL OF THE

THE JOURNAL OF THE

Annual Report

RESEARCH IN PLANT TRANSPIRATION

DA Task 3A99-27-005-08

OBJECTIVE

The objective of Task 3A99-27-005-08, "Micrometeorology (USAEPC)," is to conduct studies dealing with the physical processes involved in the exchange of energy between the atmosphere and the earth's surface. Through such basic research, knowledge of atmospheric processes will be increased and ultimately contribute to advancing the state-of-the-art in weather forecasting.

This report concerns the part of the objective which deals with the conduct of studies of the energy relations involved in the evaporation of water through the process of plant transpiration. One aspect of particular interest is the role of the stomatal mechanism in the operation of stomata; it may be possible to predict the influence of plant cover on evaporation and ultimately to exercise some control over water loss by transpiration.

AUTHORITY

Authority for this task is contained in letter, OCSigO, SIGRD-8b-5, dated 13 Aug 1957, "Proposed Coordinated Signal Corps Meteorological Program."

THE HISTORY OF

THE CITY OF BOSTON

FROM 1630 TO 1800

BY

JOHN H. COLEMAN, Esq., of the City of Boston.
In two Volumes. VOL. I.
BOSTON: PUBLISHED BY J. B. LEECH, No. 10, CORNHILL.
1840.

THE HISTORY OF THE CITY OF BOSTON, FROM 1630 TO 1800, BY JOHN H. COLEMAN, ESQ., OF THE CITY OF BOSTON. IN TWO VOLUMES. VOL. I. BOSTON: PUBLISHED BY J. B. LEECH, NO. 10, CORNHILL. 1840.

THE HISTORY OF

THE CITY OF BOSTON, FROM 1630 TO 1800, BY JOHN H. COLEMAN, ESQ., OF THE CITY OF BOSTON. IN TWO VOLUMES. VOL. I. BOSTON: PUBLISHED BY J. B. LEECH, NO. 10, CORNHILL. 1840.

SUMMARY

Characteristics and capabilities of a high light intensity, controlled-environment growth room are reported. Early tests of this growth room, using a radiation intensity equivalent to full sunlight, showed that it was possible to grow plants that were identical in appearance to field grown plants. Preliminary results of studies with these plants indicate that:

1. With radiation intensity equivalent to full sunlight, the maximum transpiration rate at 28°C. ambient temperature was approximately 125 percent of that at 18°C.
2. The transpiration rate during the light period increased with increasing radiation intensity ($0.4 \text{ cal cm}^{-2} \text{ min}^{-1}$ to $1.3 \text{ cal cm}^{-2} \text{ min}^{-1}$).
3. The transpiration rate during the light period was lower on the second day of the experiment. This decrease, which was especially evident under illumination at full sunlight equivalent, was attributed to increased soil moisture tension.
4. The transpiration rate during the light period at 18°C. decreased markedly when the relative humidity was increased from a value of 61 percent to one of 88 percent.

Furthermore, the development of special devices such as leaf chambers, a solar spectrophotometer, gas mixing systems, and a stomate camera are described.

Preliminary cellular studies by tissue culture methods to probe the mechanism of guard cell operation are described. For this purpose albino corn was successfully cultured on sucrose.

Attempts by several methods to experimentally induce guard cell opening in albino corn have been unsuccessful to date.

Guard cells of corn and bean seedlings grown in the dark accumulate starch, and small amounts of this starch are retained by the guard cells even though the plants may die due to lack of carbohydrates.

Experiments to determine the effect of foliar application of two different growth regulators on transpiration are described.

TABLE OF CONTENTS

	Page
Objective and Authority.	2
Summary.	3
Introduction and General Remarks.	7
Chapter I. Controlled Environment Facilities	8
Chapter II. Stomate Photography	30
Chapter III. Solar Spectrophotometer	36
Chapter IV. Guard Cell Action	44
Literature Cited	54

LIST OF ILLUSTRATIONS

Figure

1. Schematic diagram showing one of three incandescent bulb layouts in growth room nr 1.	10
2. Maximum radiant energy in growth room as a function of distance from the ceiling.	11
3. Radiant energy output from spot lamps as influenced by voltage.	12
4. Effect of depth of water in heat filter on available radiant energy in growth room at 100 centimeters from ceiling.	14
5. Effect of depth of water on spectral distribution of available radiant energy from incandescent bulbs.	15
6. A red kidney bean leaf enclosed in a leaf chamber for measurement of carbon dioxide and moisture vapor exchange between the leaf and a controlled environment	18
7. Gas mixing system	19
8. Red kidney bean plants grown in master growth room	21

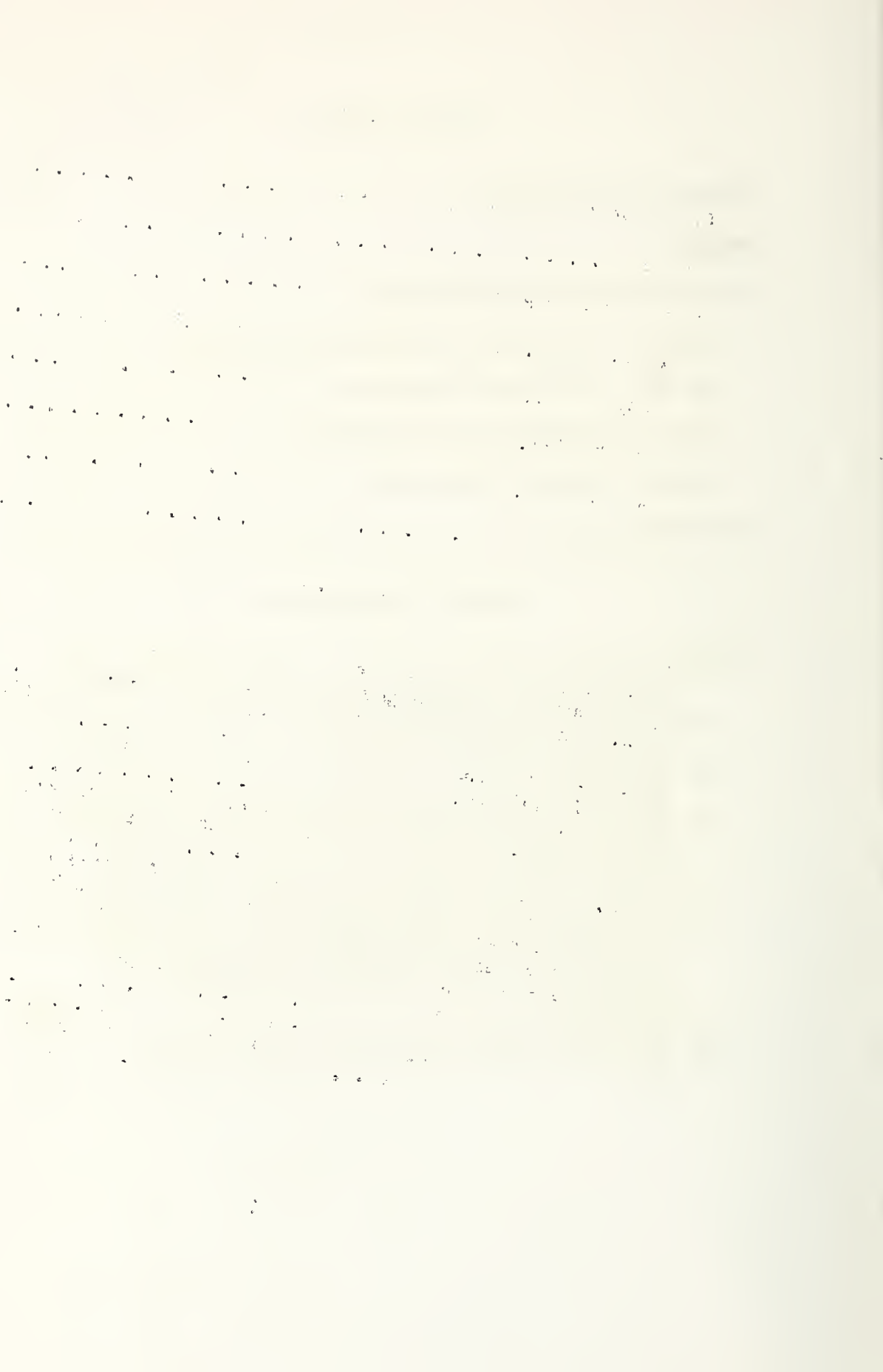


TABLE OF CONTENTS (Continued)

LIST OF ILLUSTRATIONS (Continued)

Figure	Page
9. Red kidney bean plant internodes decreased in length with increasing light intensity	22
10. The effect of light intensity on the total leaf area of red kidney bean plants	23
11. Transpiration of red kidney beans increased with increasing light intensities regardless of previous treatment	24
12. Rate of transpiration of red kidney bean plants when temperature was held at 18° C. and relative humidity at 61% for the entire 28-hour period.	26
13. Rate of transpiration of red kidney bean plants when temperature was held at 18° C. and relative humidity at 88% for the entire 28-hour period.	27
14. Rate of transpiration of red kidney bean plants when temperature was held at 18° C. and relative humidity at 61% for the entire 28-hour period.	28
15. Rate of transpiration of red kidney bean plants when temperature was held at 28° C. and relative humidity at 91% for the entire 28-hour period.	29
16. An Exakta single lens reflex camera as adapted for photographing plant stomates.	31
17. A detailed drawing showing the construction of the stomate camera.	32
18. Open stomates of a red kidney bean plant.	34
19. Solar Spectrophotometer	37
20. Integrating spectrophotometer optics.	39
21. Integrating spectrophotometer circuitry	40
22. Albino corn seedlings fed by periodically cutting leaves and immersing in .3M sucrose	46
23. Albino guard cells opened by Tween 20 and sucrose treatment	47
24. Typical lysis of cells in area of Tween 20 and sucrose treatment	48

TABLE OF CONTENTS (Continued)

LIST OF ILLUSTRATIONS (Continued)

Figure		Page
25.	Stoma of etiolated bean plant; dark object in each guard cell are starch grains derived from sucrose feeding	50
26.	Transpiration loss of red kidney bean plants treated at indicated concentrations with 2,4-dichlorophenoxy-acetic acid	52
27.	Transpiration loss of red kidney bean plants treated at indicated concentrations with β -naphoxyacetic acid	53

LIST OF TABLES

Table

I.	Light quality in the growth room from 300-watt incandescent spot lamps as a function of voltage variations on the lamps	16
----	---	----

ANNUAL REPORT
of
RESEARCH IN PLANT TRANSPIRATION

INTRODUCTION AND GENERAL REMARKS

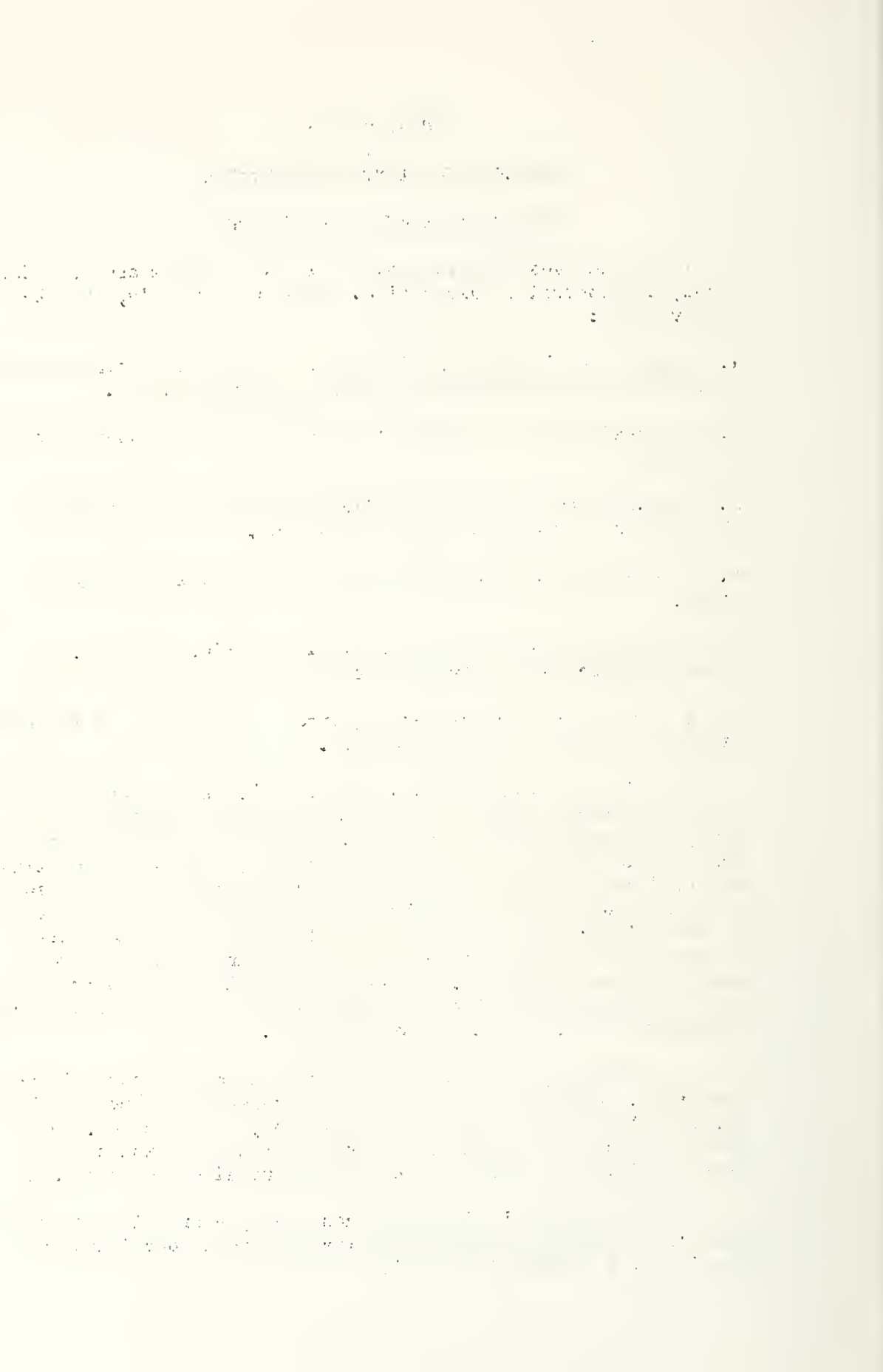
The objectives of this project are to better measure, understand, and control transpiration. More specifically, the objectives are:

1. To measure the effects of radiant energy, temperature, humidity, and other environmental factors on transpiration.
2. To develop better methods and techniques for measuring transpiration.
3. To gain knowledge of the cellular processes and factors which control or affect guard cell action.
4. To observe and accurately measure the reactions of guard cells.
5. To discover and evaluate chemical, genetic, physical, or other means to control transpiration.
6. To develop instruments and equipment which will aid in fulfilling the above-listed objectives.

In order to undertake this study, it has been necessary to construct growth rooms, CO₂ and H₂O mixing and monitoring systems, to develop leaf and plant chambers, to develop an instrument for accurately measuring the intensity and quality of light, and to develop methods of analyzing and recording the movement of stomata by microphotography. An integral part of the study at the cellular level is aimed at understanding the mechanism of guard cell action. If we can find and understand the reasons for their movements, we will be much closer to controlling their action and thus improving the water economy of plants and understanding the immediate microclimate.

The following report summarizes the accomplishments of the past year. Most of the efforts of the researchers involved have necessarily been channeled into designing, constructing, and testing special equipment to be used in transpiration studies. Some preliminary transpiration research results are reported.

A comprehensive bibliography has been prepared in connection with this project on plant transpiration and is published as Supplement I to USAEPG 6-42-61.



CHAPTER I

CONTROLLED ENVIRONMENT FACILITIES

General Remarks.

One of the principal research facilities at this location is the high light intensity controlled environment master growth room, 17.8 feet long by 12.2 feet wide by 7.0 feet high. Automatic controls permit programming of 24-hour cycles of varying temperature, relative humidity, and light intensity. It is possible with these controls to establish any desired environmental pattern within the limits of the system.

The range on the temperature controls is from 5 to 50 degrees centigrade. Humidity controls can achieve preselected conditions ranging from 10 to 90 percent relative humidity. Air exchange within the room can be varied from 5 volumes per hour to replacement approximately once each hour.

Lighting System for Master Growth Room.

The lighting system in the master growth room utilizes incandescent spot lamps instead of fluorescent tubes, and merits detailed discussion.

It contains three light banks each of which is 6 feet long and 4 feet wide. Each bank is lighted by ninety-six 300-watt incandescent spot lamps, Sylvania 300R/2SP, with extended metal base. There are 8 rows of lamps with 12 bulbs per row, spaced 6 inches apart between rows and between bulbs within rows. The lamps are located with their lenses 12 inches above the ceiling of the growth room and are sealed off from the growth room by tempered plate glass. The major part of the heat is dissipated from the bulbs by circulating 10,000 cubic feet per minute of outside air through the lamp chamber. An additional portion of the heat is absorbed by water that is circulated over the glass.

The light intensity control system operates on the principle of driving one-half of the bulbs to full intensity by means of a rheostat. After the variable bulbs have reached full intensity, the remaining bulbs are turned on to full intensity

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

100

and the bulbs on the rheostat simultaneously cut off. For intensities greater than one-half maximum, the lights on the rheostat are again brought up to maximum intensity at 115 volts. For a schematic layout of the bulb arrangement, refer to figure 1.

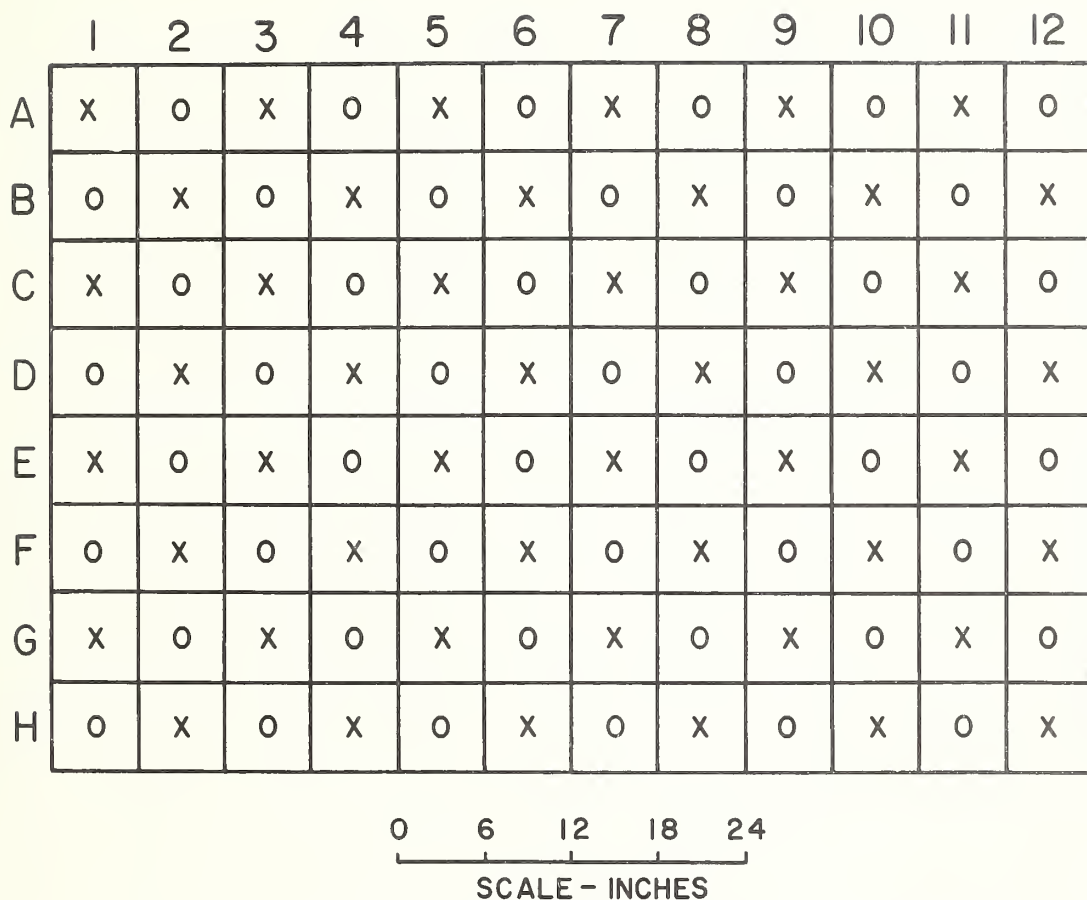
Light Measurements.

Measurements of total radiant energy have been made with Beckman-Whitley total radiometers, Eppley pyrheliometers, and an Eppley thermopile. These data indicate an intensity of $1.55 \text{ cal cm}^{-2} \text{ min}^{-1}$ can be achieved at a distance of 40 centimeters from the ceiling of the growth room. This is equivalent to full sunlight and means that controlled experiments can be performed at any energy level that is possible on earth. This is a significant capability since the lighting systems of most growth rooms have been non-variable with maximum intensities of 40 percent full sunlight.

Figure 2 illustrates the maximum obtainable radiant energy in the growth room as influenced by the distance from the ceiling. Data are not given for distances closer than 40 centimeters since the light intensity at this point is equivalent to full sunlight. Furthermore, it is desirable to keep the growing plants at least 40 centimeters below the ceiling so that air can flow freely over them. It is significant that the light intensity levels off at about 120 centimeters from the ceiling, since the area is receiving the equivalent of parallel light from a source at an infinite distance. The intensity at this level-out point is $1.09 \text{ cal cm}^{-2} \text{ min}^{-1}$, which is adequate for many experiments.

In order to program a diurnal cycle of light intensities, it is essential to know the various parameters affecting light output. The voltage on the incandescent bulbs and the depth of the water in the heat filter are the 2 variables which must be considered.

The effect of voltage on light output from the incandescent bulb is shown in figure 3. Measurements were taken with a Beckman-Whitley total radiometer and an Eppley pyrheliometer. The results are expressed as percent of the maximum light output at 115 volts. It can be seen from this figure that the light output can be easily controlled by controlling the voltages applied to the bulbs.



CODE- INCANDESCENT BULB LOCATION

O- FIXED VOLTAGE BULBS

X- VARIABLE VOLTAGE BULBS

Figure 1. Schematic diagram showing one of three incandescent bulb layouts in growth room nr 1.

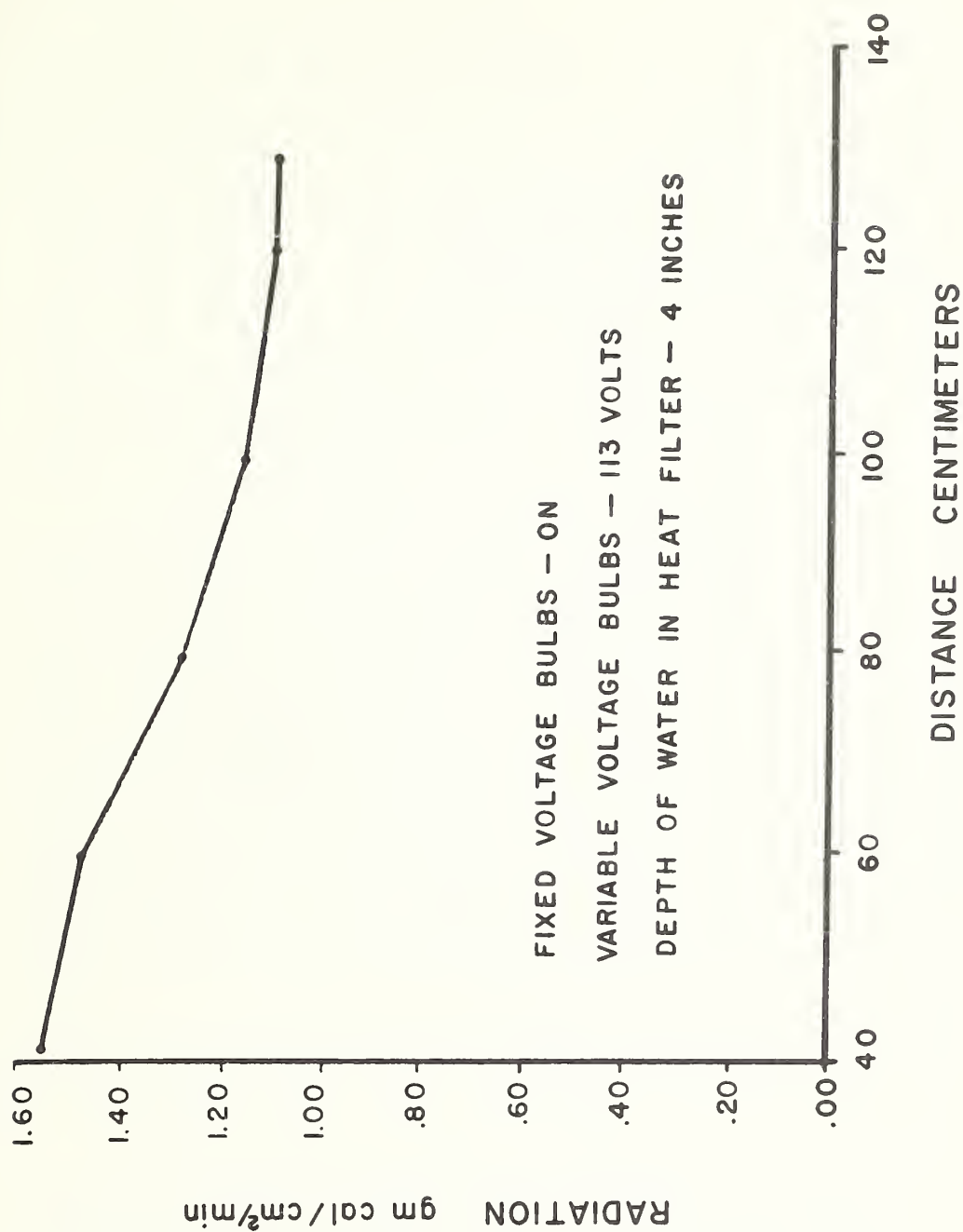


Figure 2. Maximum radiant energy in growth room as a function of distance from the ceiling.

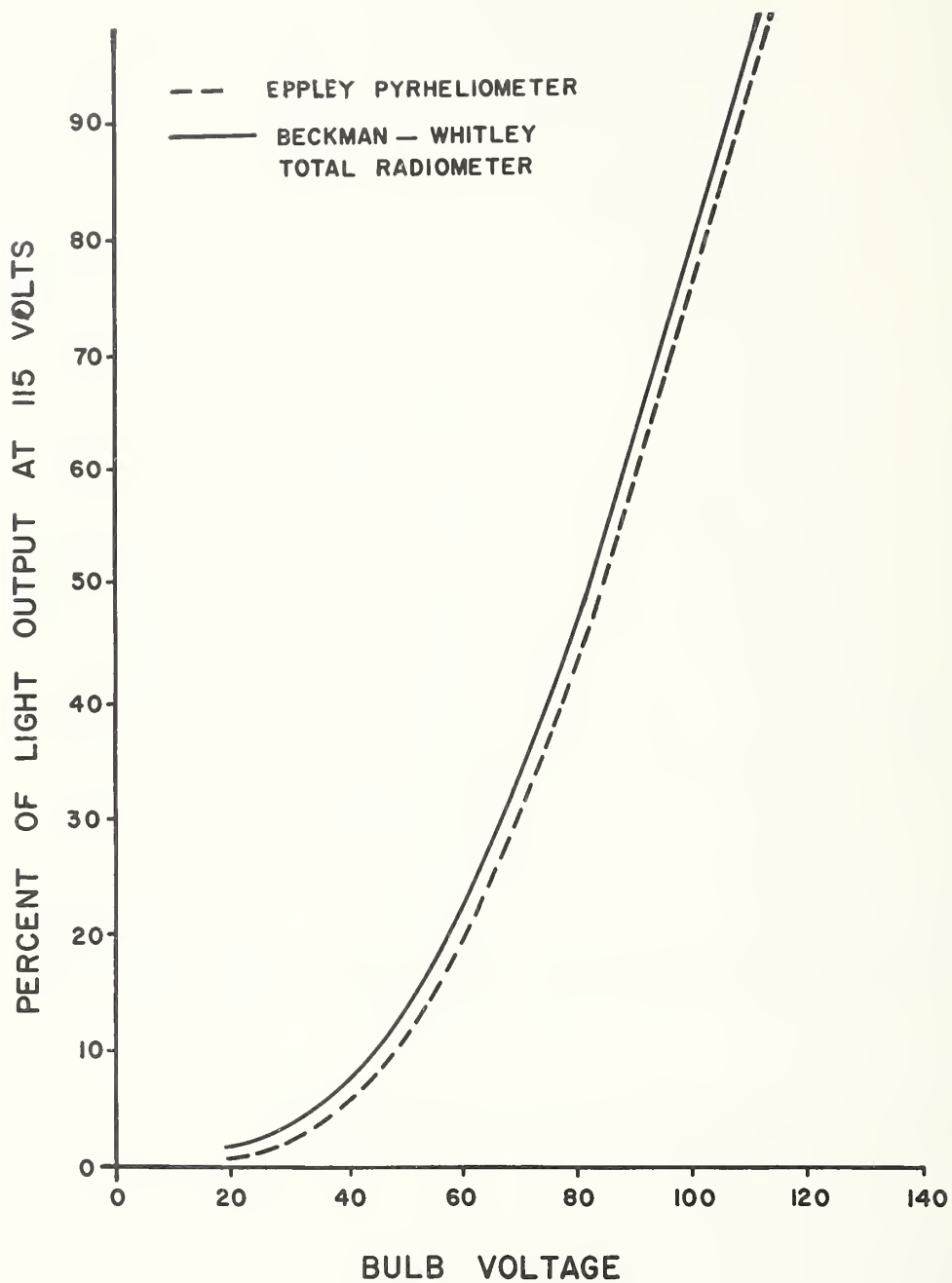


Figure 3. Radiant energy output from spot lamps as influenced by voltage.

The influence of depth of water in the heat filter upon total energy available in the growth room is illustrated in figure 4. This figure shows that the maximum light intensity at 100 centimeters from the ceiling can be varied from 1.45 to 1.07 cal cm⁻² min⁻¹ by adjusting the water level in the heat filter. This fact will permit adjustments for bulb aging without having to change the control cams on the automatic programing system. The effect of aging on bulb output is unknown at this time, but it is expected to be small. Preliminary data indicate no detectable reduction in output after 350 hours of continuous operation. All bulbs used to collect the data reported here had been operated at least 700 hours before measurements were made. The reported light intensity values should therefore be considered reasonable estimates for at least 75 percent of the expected life of 2,000 hours.

Light quality is known to affect the physiological processes of growth in plants. It is important therefore to know how much the spectral distribution of light in the growth room is altered by varying the depth of water in the heat filter. Figure 5 illustrates the effect of depth of water on the spectral distribution of light transmitted through the water from one of the incandescent spot lamps used in the growth room. The entire spectrum was divided into 6 regions by the use of 5 cut-off filters. It can be seen that light in the infrared region is sharply reduced as the first 3 inches of water are added. After the initial 3-inch depth has been reached, the light quality is relatively unaffected by additional increments of water except for the long wave radiation of greater than 970 millimicrons. Since the average operating level in the filters is 4 inches, the light quality will remain fairly constant during any fluctuations in the water level around this average value.

For special light quality experiments, it will be possible to increase the amount of infrared by lowering the water level in the filters.

Another important consideration of the lighting system is the effect of the bulb voltage on light quality. Preliminary data indicate this effect is relatively small for all intensities greater than 25 percent full intensity. Below this level the amount of red and infrared increases because of the low voltage across the bulbs. The data for this effect of bulb voltage on light quality are given in table I.

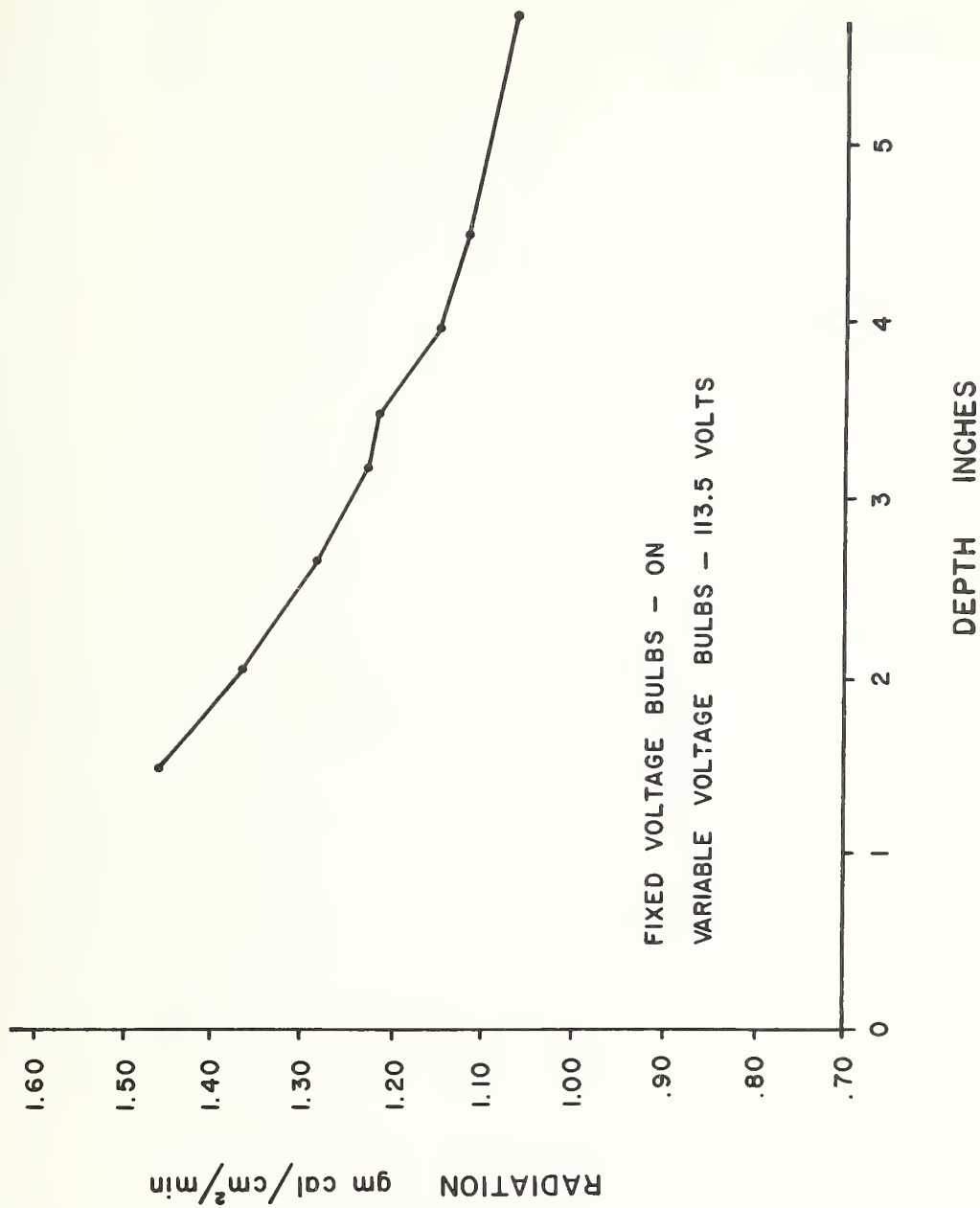


Figure 4. Effect of depth of water in heat filter on available radiant energy in growth room at 100 centimeters from ceiling.

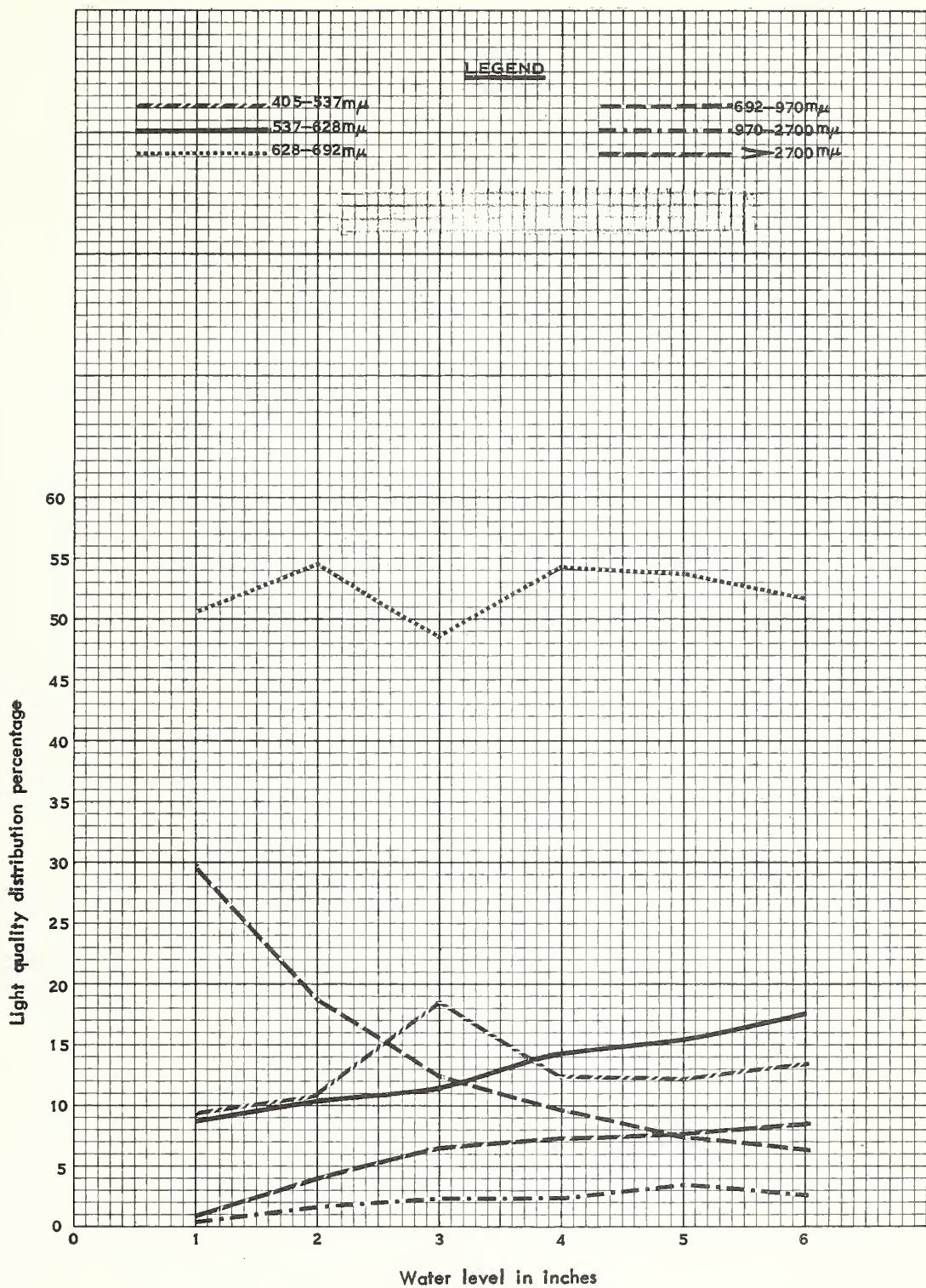


Figure 5. Effect of depth of water on spectral distribution of available radiant energy from incandescent bulbs.

TABLE I

Light quality in the growth room from 300-watt incandescent spot lamps as a function of voltage variations on the lamps. (All values are expressed as percent of total radiant energy.)

Wave Length	Variable 113 Volts Fixed: ON	Variable 60 Volts Fixed: ON	Variable 80 Volts Fixed: OFF	Variable 48 Volts Fixed: OFF
Less than 405 mμ	0	0	1	0
405-537 mμ	7	8	4	0
537-628 mμ	20	20	17	15
628-692 mμ	17	17	15	11
692-970 mμ	49	49	54	62
Longer than 970 mμ	7	6	9	12

Pre-conditioning Environment Chambers.

Three small "walk-in" type refrigerators were converted into plant growth chambers, with minimum lighting. These chambers are used to start large populations of seedlings under reproducible, controlled conditions. They are later sorted for uniformity and moved to the master climate-control room for further conditioning and treatment in transpiration studies.

Leaf Chambers

Certain transpiration studies require accurate control and measurement of temperature, carbon dioxide concentration, relative humidity, and other factors surrounding a single leaf instead of a plant or group of plants. This requires that the leaf be enclosed in a small chamber through which gases may be circulated and light introduced. It is also desirable to photograph stomate activity through the chamber wall without interfering with the leaf microclimate. Figure 6 shows an experimental leaf chamber which has been constructed for this purpose. The sides and top of the chamber are constructed of plexiglas. The bottom consists of blackened copper plate. Attached to the lower side of the copper plate is a copper coil through which water is circulated to control the temperature inside the leaf chamber. Along each side of the chamber are manifolds through which gases are introduced and exhausted. Tests have shown that the flow of gases through the chamber is sufficiently uniform along the entire length of the chamber. Nylon threads stretched across the chamber support the leaf and hold it away from the sides of the chamber.

Gas Mixing and Monitoring System.

A gas mixing system has been developed to supply predetermined mixtures of gases to leaf chambers for transpiration, photosynthesis and stomatal behavior experiments. The system is designed to handle flow rates from 0.005 to 1,000 liters per hour with an accuracy of better than 1 percent for all flow rates. It is designed to vary the vapor pressures of carbon dioxide and water while holding oxygen and nitrogen constant at the levels found in air. The schematic of the system is given in figure 7. Flow is controlled by pressure drop across precisely calibrated capillaries and orifices. Operating pressures range from 5 to

THE HISTORY OF THE

1780

of the City of New York, from the first settlement of the Dutch in 1624, to the present time. The history of the city is divided into three periods: the first, from 1624 to 1674, when the city was under the Dutch; the second, from 1674 to 1784, when it was under the English; and the third, from 1784 to the present time, when it was under the Americans.

The first period of the history of the city is the most interesting, as it shows the city in its infancy, and the struggles it underwent to become a great city. The Dutch, who were the first settlers, found the city a swampy and unhealthy place, but they persevered, and in 1624 they established a settlement on the island of Manhattan. The city grew rapidly, and by 1674 it had become one of the most important cities in the colonies. The English, who took possession of the city in 1674, found it a well-established city, and they continued to develop it. The city grew even more rapidly, and by 1784 it had become one of the largest and most important cities in the United States.

THE HISTORY OF THE

City of New York, from the first settlement of the Dutch in 1624, to the present time. The history of the city is divided into three periods: the first, from 1624 to 1674, when the city was under the Dutch; the second, from 1674 to 1784, when it was under the English; and the third, from 1784 to the present time, when it was under the Americans.

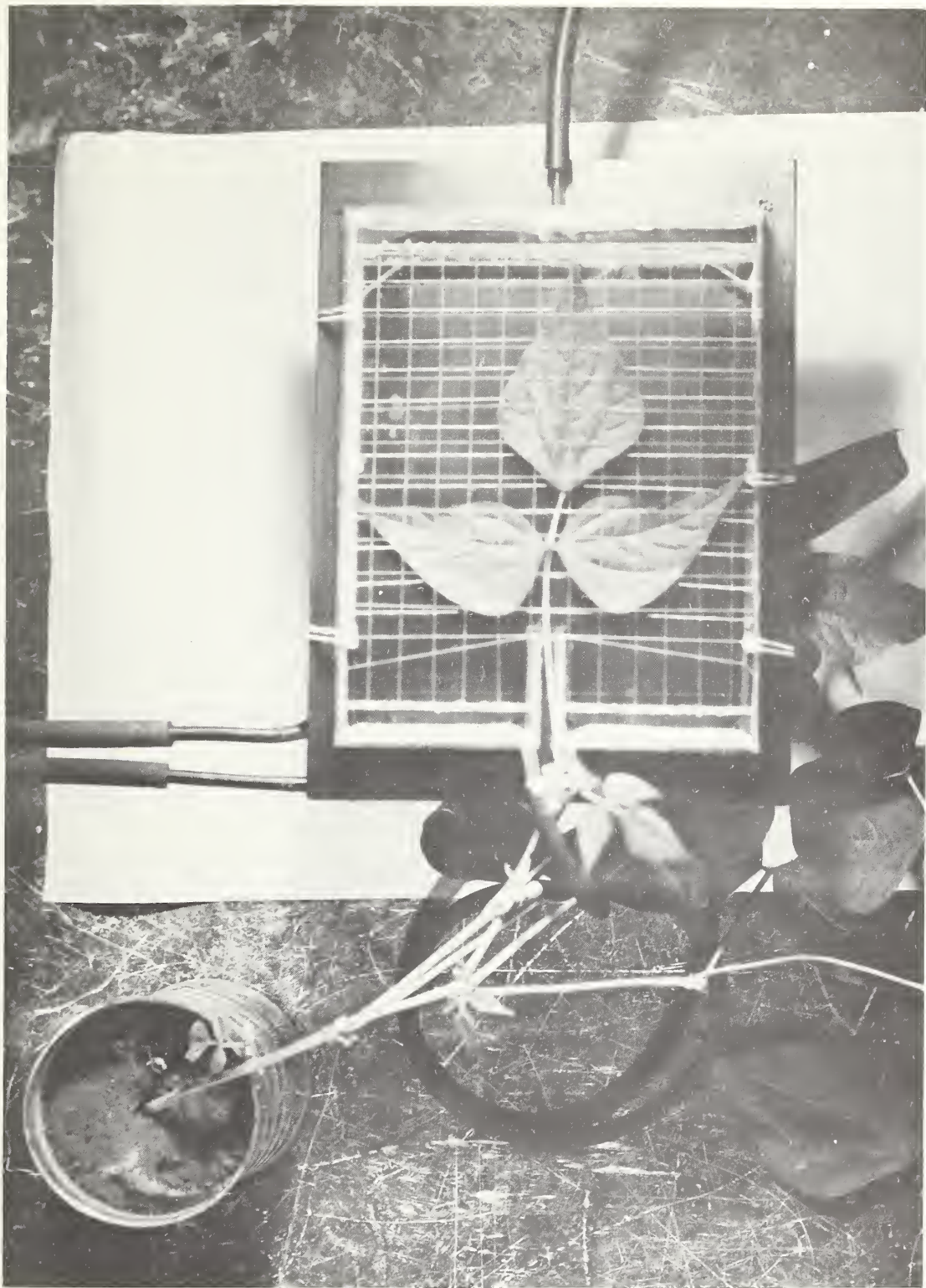


Figure 6. A red kidney bean leaf enclosed in a leaf chamber for measurement of carbon dioxide and moisture vapor exchange between the leaf and a controlled environment.

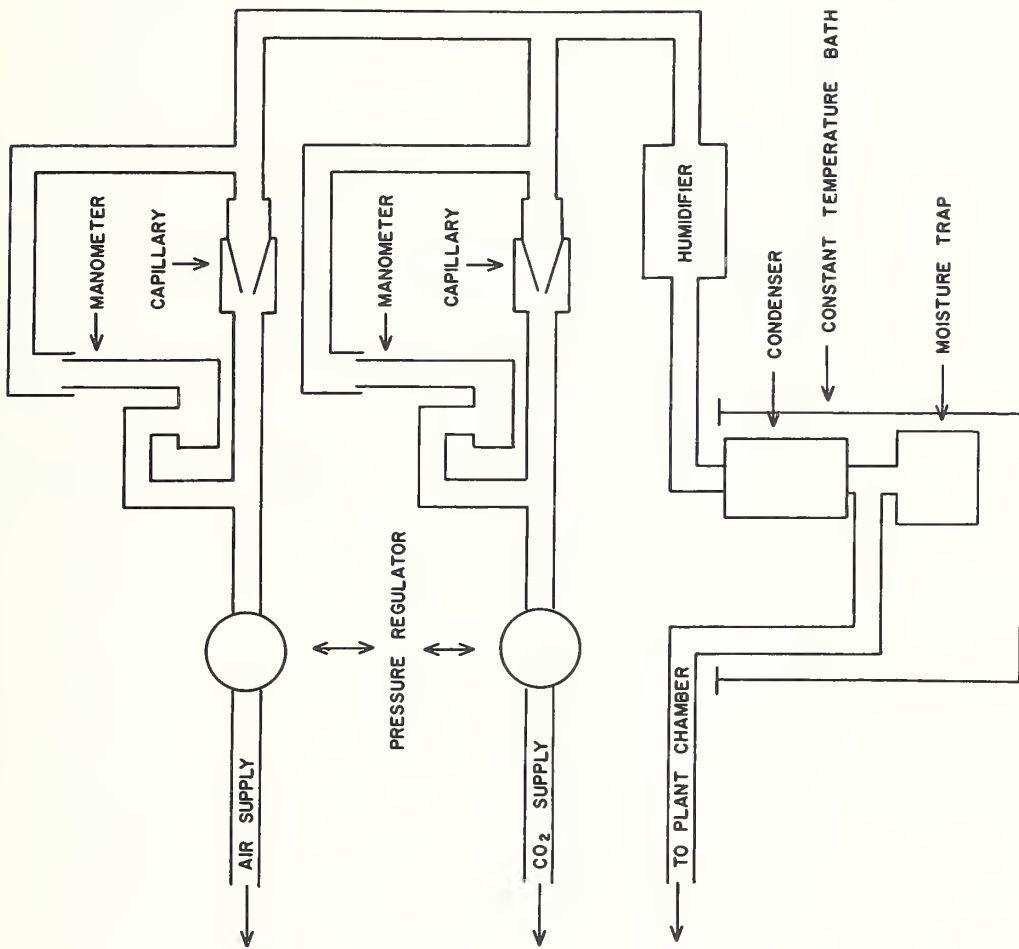


Figure 7. Gas mixing system.

100 millibars and are controlled to ± 0.05 millibars.

The initial step in gas mixing is to mix dry, carbon dioxide free air and carbon dioxide in amounts which will give the desired vapor pressure of carbon dioxide in the final mixture. The amounts of each gas will depend upon the flow rate desired, the barometric pressure, and the desired vapor pressure of water. Carbon dioxide is removed from the air supply so as to eliminate a variable and permit easy blending of gas mixtures to attain lower concentrations of carbon dioxide than are normally found in air.

Once the gas is mixed it is passed through a humidifier at an elevated temperature so as to insure adequate humidification. The gas is then passed through a cooling coil in a constant temperature bath to condense the excess water and reduce it to the desired vapor pressure. As the air leaves the cooling coil, the vapor pressures of all the component gases of the mixture are at their desired values. The gas is warmed to the desired temperature in a heat exchanger and then flows to the desired leaf or plant chamber.

Vapor pressures of carbon dioxide and water are monitored with Beckman 15-A infrared analyzers. The carbon dioxide analyzer is designed to operate over different ranges of vapor pressure. The minimum range is from 0 to 300 microbars, and the maximum range is from 0 to 1,800 microbars of carbon dioxide. Accuracy is 2 percent of full scale for all ranges.

The water analyzer is designed to operate over the range from 0 to 45 millibars and is accurate to 2 percent of full scale.

Preliminary Plant Growth Results.

Due to their sensitivity to light, red kidney bean plants were used as test plants for preliminary growth room work (fig. 8). These tended to be shorter with increasing light intensity due to differences in internode length (fig. 9). Leaf area was greater under an intermediate light treatment than under either extreme treatment (fig. 10). Preliminary transpiration studies were conducted on more than 100 plants. Transpiration increased with increasing light intensity for all plants studied, regardless of previous treatment received (fig. 11).



Figure 8. Red kidney bean plants grown in master growth room. Plants are the same age but received different intensities of the same quality of light. Reading from left to right they receive $1/4$, $1/2$, and full intensity ($1.3 \text{ cal cm}^{-2} \text{ min}^{-1}$ at bench height). The plant on the right, which received full intensity, closely resembles plants grown under field conditions.

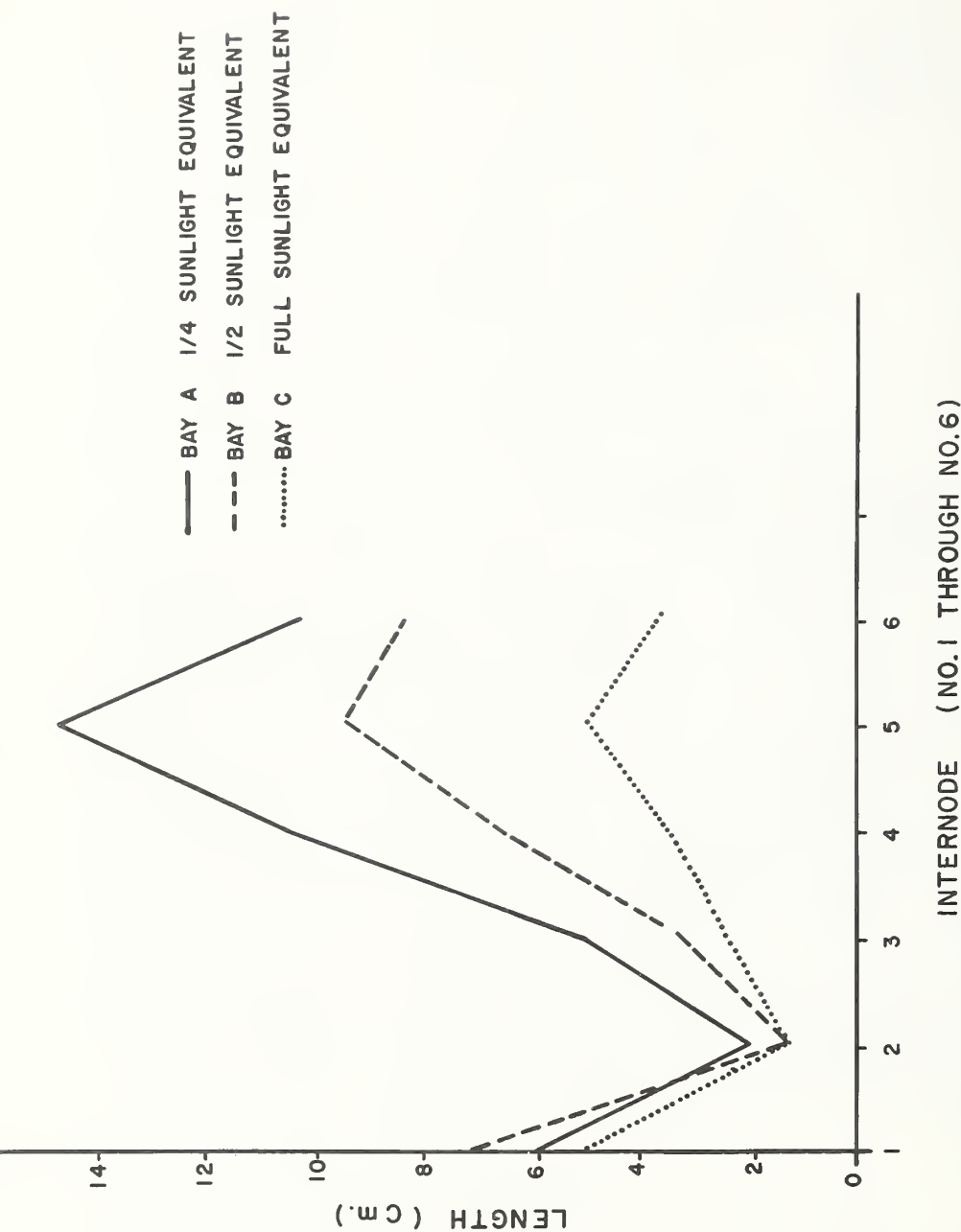


Figure 9. Red kidney bean plant internodes decreased in length with increasing light intensity. The intensity was varied without changing light quality. Full sunlight equivalent for this study was $1.3 \text{ cal cm}^{-2} \text{ min}^{-1}$.

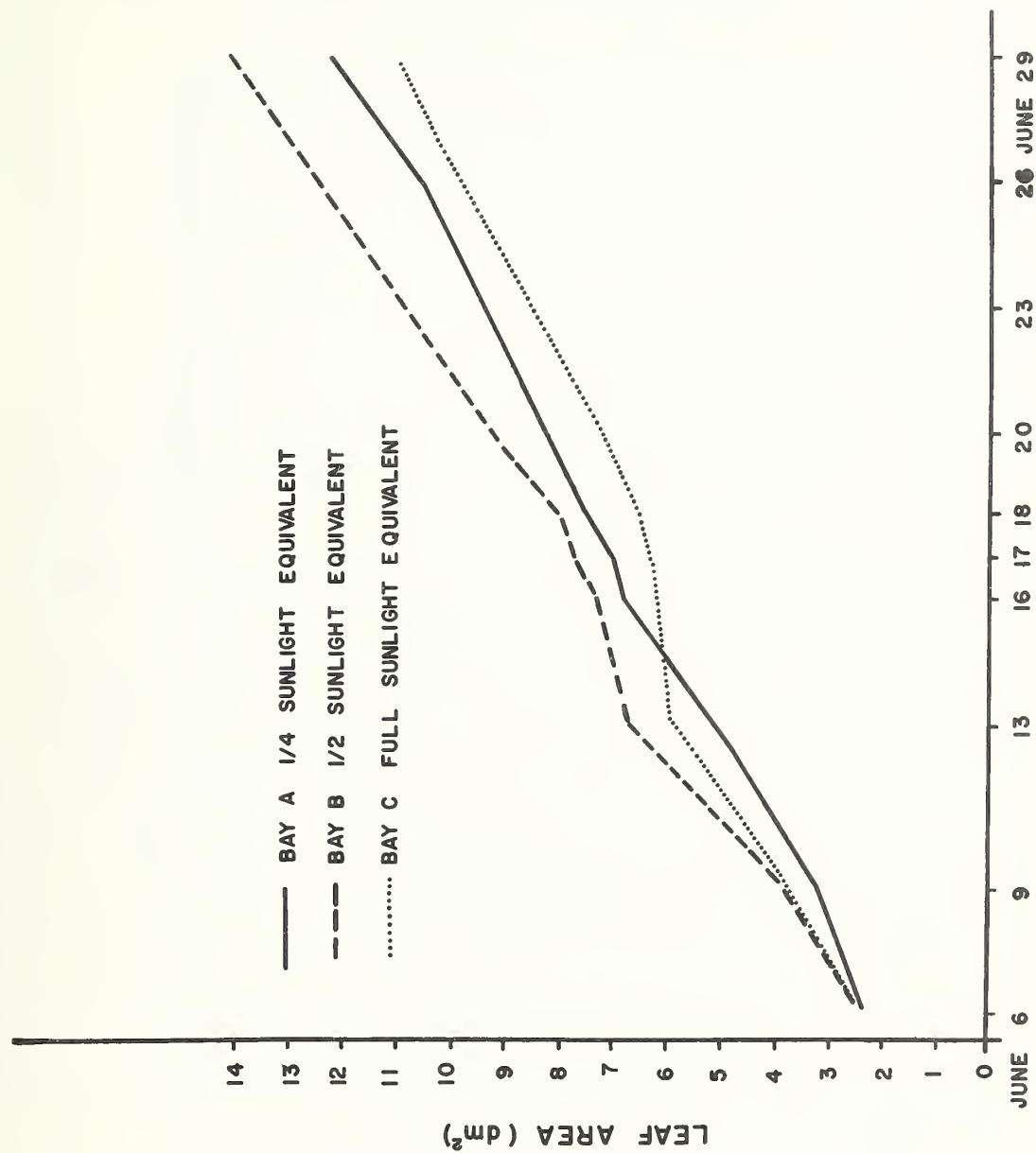


Figure 10. The effect of light intensity on the total leaf area of red kidney bean plants. Full sunlight equivalent for this study was $1.3 \text{ cal cm}^{-2} \text{ min}^{-1}$.

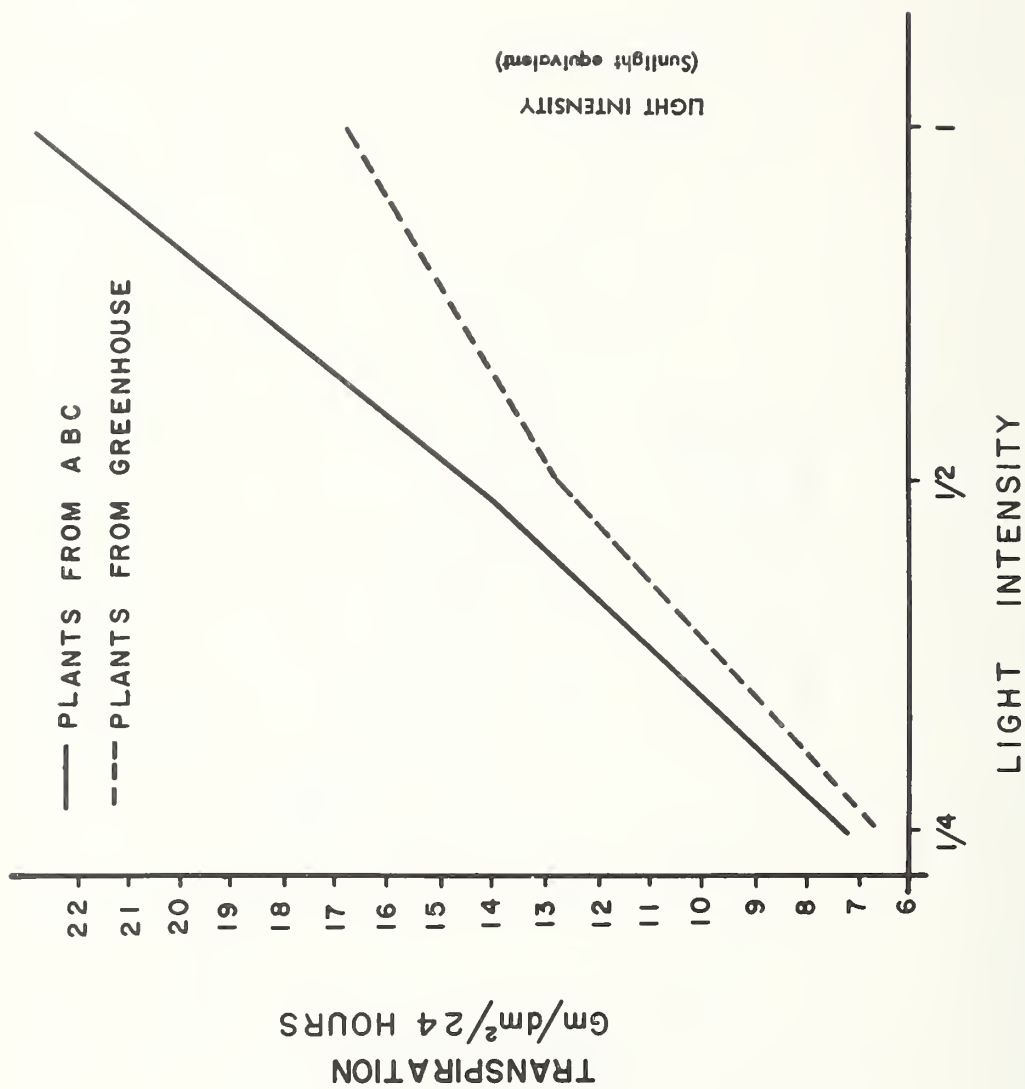


Figure 11. Transpiration of kidney beans increased with increasing light intensities regardless of previous treatment.

Four short preliminary studies were conducted with plants of similar backgrounds carefully sorted for uniformity. Temperature and humidity were held constant for the 2 days preceding the study and during the 28-hour period during which data were taken. Sunlight equivalent was $1.3 \text{ cal cm}^{-2} \text{ min}^{-1}$.

Ten red kidney bean plants were used in each light treatment. Light was programmed so that treatment began at 7:00 a.m. with the intensity gradually increasing to full treatment intensity by 9:30 a.m., remaining at this level until 4:30 p.m. when it gradually decreased to zero light on all treatments at 6:00 p.m. Plants were sub-irrigated during the night preceding each transpiration study.

In general, transpiration increased in all bays up to midday, and then declined until 8:00 p.m. (fig. 12). The transpiration peak was not as high the second day as on the first, due to increased soil moisture tension. The higher the light intensity, the greater the rate of transpiration. During darkness, any differences were too small to be detected.

An increase of relative humidity from 61 percent (fig. 12) to 88 percent (fig. 13) at 18°C . produced a marked decrease in the rate of transpiration for all bays during the daylight hours. The curves in figure 14 are derived from a rerun of 18°C ., and 61 percent relative humidity with the same plant population used for figure 12. On the second run, the plants were larger; thus they used greater quantities of water in a given period from a fixed reservoir (2,000 grams soil). The decrease in transpiration the second day under full sunlight equivalent (fig. 14) is a reflection of decreased water availability. The results attest to the reproducibility of the experimental conditions. Some of the blips in the curves are evidently within experimental error and little emphasis should be given these until further statistical analysis has been made. The increase in temperature from 18°C . (fig. 12) to 28°C . (fig. 15) resulted in marked increases of day transpiration at full sunlight intensity. The transpiration at 28°C . would probably have been higher than that recorded had the vapor pressure deficit at 28°C . been comparable to that at 18°C . Night transpiration was only slightly affected.

...the ... of ...
...the ... of ...
...the ... of ...
...the ... of ...

...the ... of ...
...the ... of ...
...the ... of ...
...the ... of ...

...the ... of ...
...the ... of ...
...the ... of ...
...the ... of ...

...the ... of ...
...the ... of ...
...the ... of ...
...the ... of ...

...the ... of ...
...the ... of ...
...the ... of ...
...the ... of ...

...the ... of ...
...the ... of ...
...the ... of ...
...the ... of ...

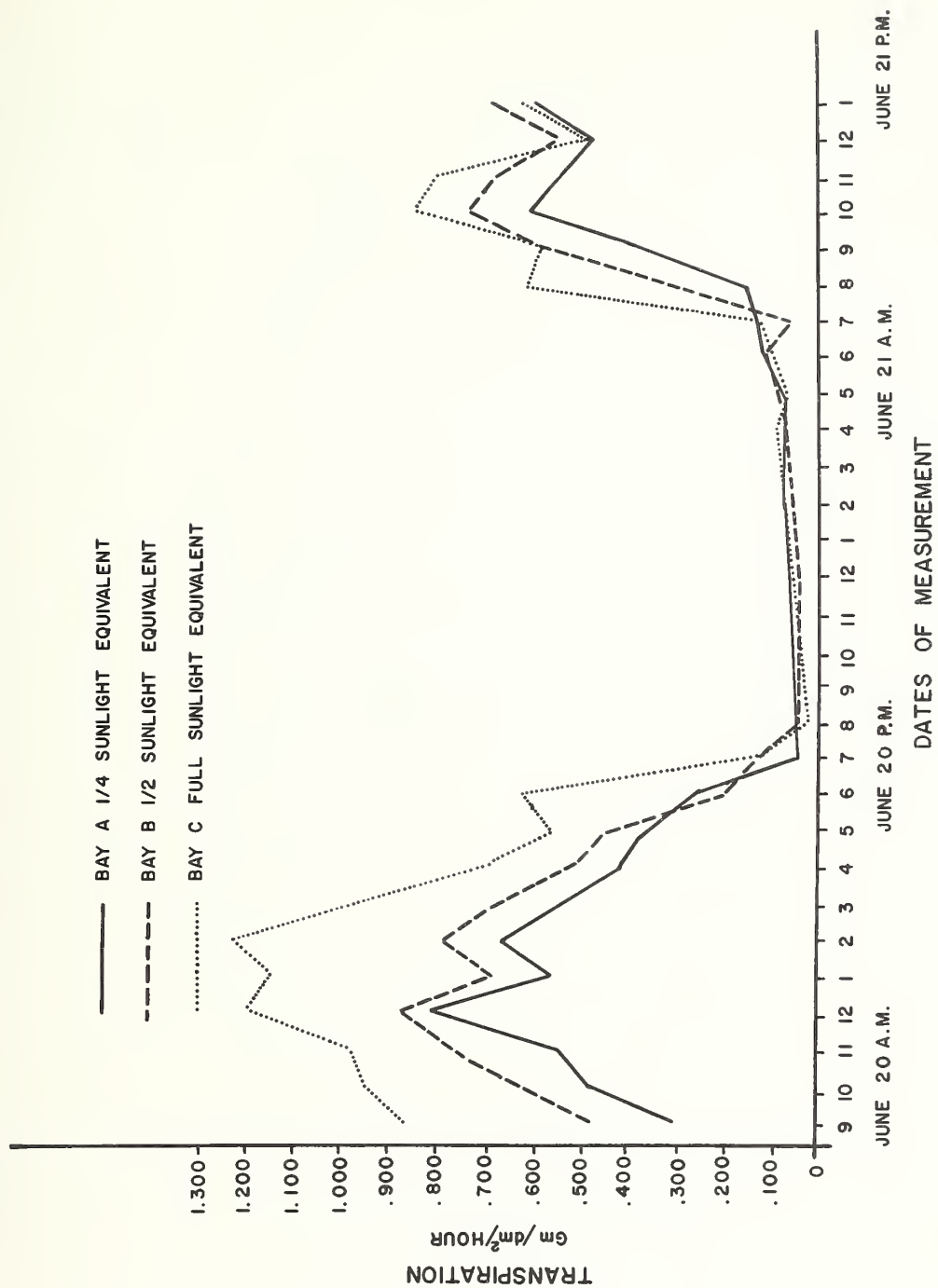


Figure 12. Rate of transpiration of red kidney bean plants when temperature was held at 18°C. and relative humidity at 61% for the entire 28-hour period.

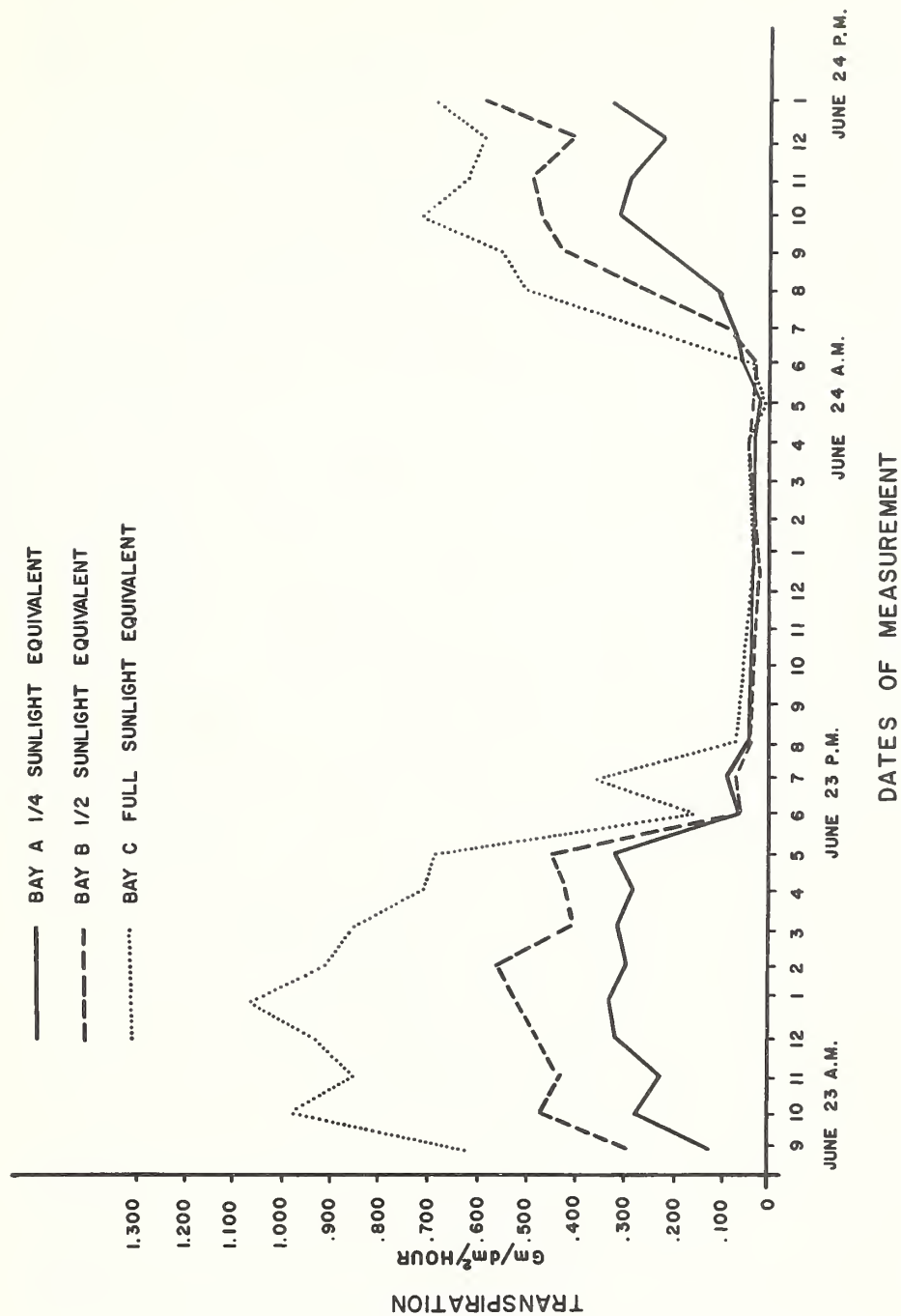
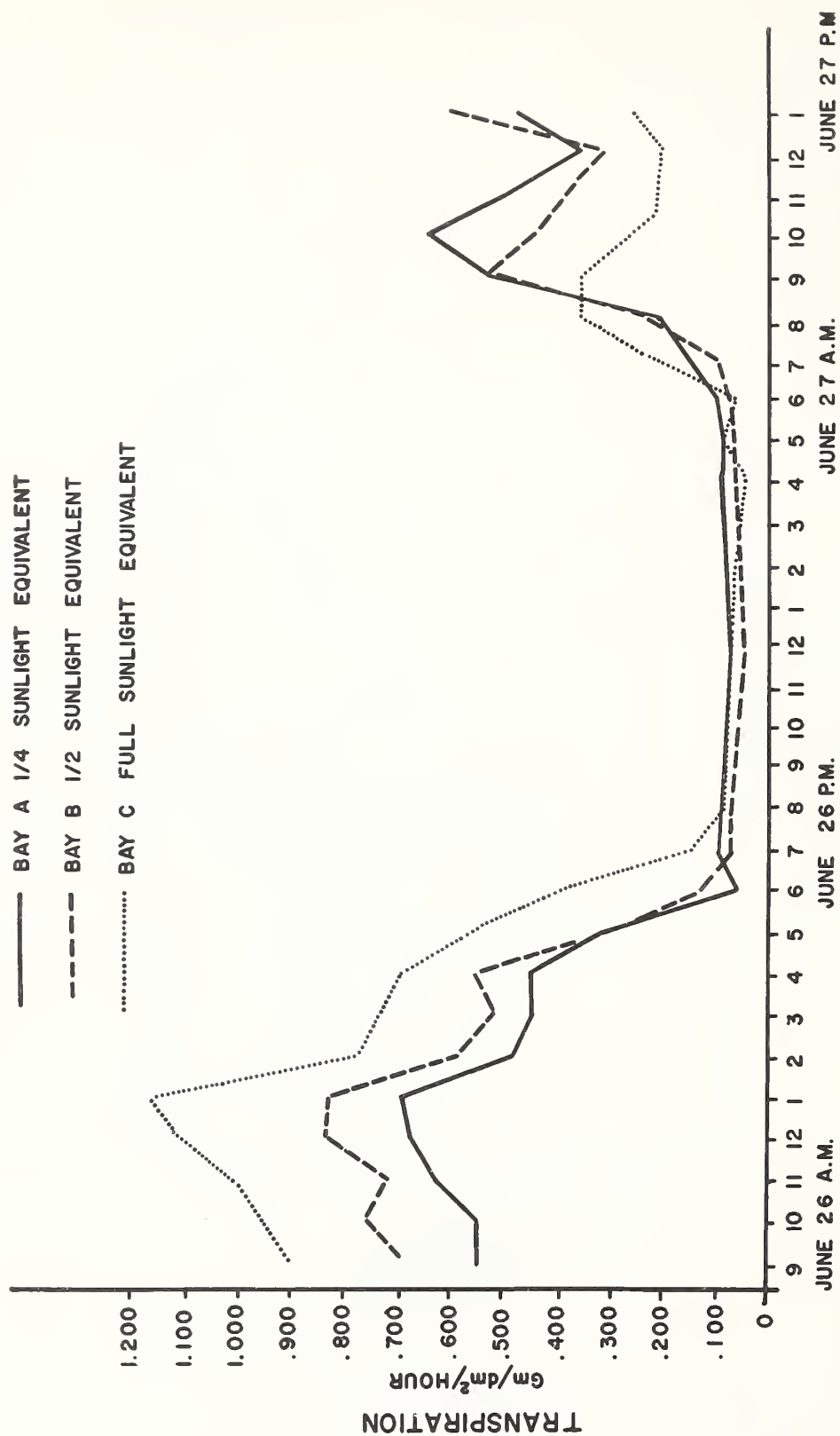


Figure 13. Rate of transpiration of red kidney bean plants when temperature was held at 18°C. and relative humidity at 88% for the entire 28-hour period.



DATES OF MEASUREMENT

Figure 14. Rate of transpiration of red kidney bean plants when temperature was held at 18°C. and relative humidity at 61% for the entire 28-hour period.

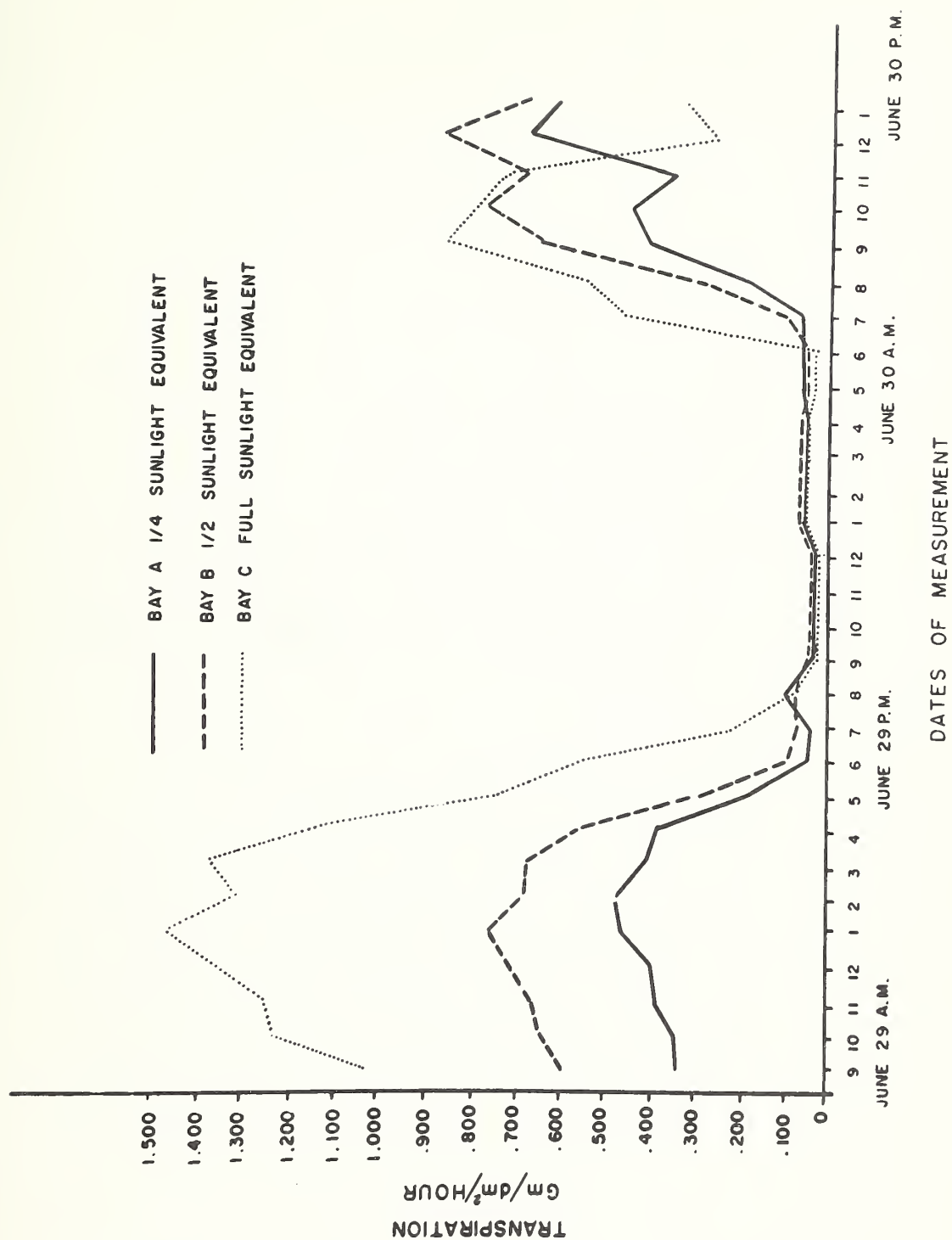


Figure 15. Rate of transpiration of red kidney bean plants when temperature was held at 28°C. and relative humidity at 91% for the entire 28-hour period.

CHAPTER II

STOMATE PHOTOGRAPHY

General Remarks.

Various techniques have been employed in attempts to measure the openings of plant stomates. Lloyd (7) removed strips of epidermis from leaves and quickly plunged the epidermis into absolute alcohol to fix the stomates for future microscopic examination. Darwin and Pertz (3), Knight (5), Spanner (11), and Williams (15) used viscous air flow and resistance porometers to obtain indirect estimates of the degree of stomatal openings of leaves through measurements of the movement of air or other gases through the leaf. The infiltration of various organic compounds into the leaf through the stomates is another indirect method of estimating stomatal opening which was employed by Williams (15), Heath (4), and Alvin and Havis (1). Anderson, *et al.* (2), Livingston and Shreve (6), and Virgin (14) have used hygrometers and hygrometric paper for detection of moisture transpired by the leaf in attempts to determine stomatal behavior and degree of opening. All of these methods have proven useful and have served as tools in the collection of valuable information regarding stomatal behavior; however, they either injure the plant or seriously alter its environment.

Stomate Camera.

A method was needed for observing and accurately measuring stomates which would disturb the plant and its environment as little as possible. The method was to be one which could be employed in a growth room, greenhouse, or in the field, and could be used to photograph either leaves in the open or leaves enclosed in leaf chambers. After consultation with research and development personnel in the optics and photography industry, and other researchers, an Exakta single lens reflex 35-mm camera was adapted as shown by the photograph (fig. 16) and the drawing (fig. 17). Basically, the "stomate camera" consists of an Exakta camera body in which the camera lens has been replaced with microscope optics. The optics are a Zeiss Neofleur 6.3/2.0 objective and a Bausch and Lomb 20X hyperplane eyepiece. The relatively low power objective was used to maintain a large working distance, depth of field, and field

The first part of the paper discusses the importance of the study of the history of the United States. It is argued that a knowledge of the past is essential for a full understanding of the present. The author then proceeds to discuss the various factors that have shaped the development of the United States, including the role of the government, the influence of the economy, and the impact of the culture. The author concludes by stating that the study of the history of the United States is a task of great importance and one that should be undertaken by all who are interested in the future of the country.

• 2 •

The second part of the paper discusses the importance of the study of the history of the United States. It is argued that a knowledge of the past is essential for a full understanding of the present. The author then proceeds to discuss the various factors that have shaped the development of the United States, including the role of the government, the influence of the economy, and the impact of the culture. The author concludes by stating that the study of the history of the United States is a task of great importance and one that should be undertaken by all who are interested in the future of the country.



Figure 16. An Exakta single lens reflex camera as adapted for photographing plant stomates.

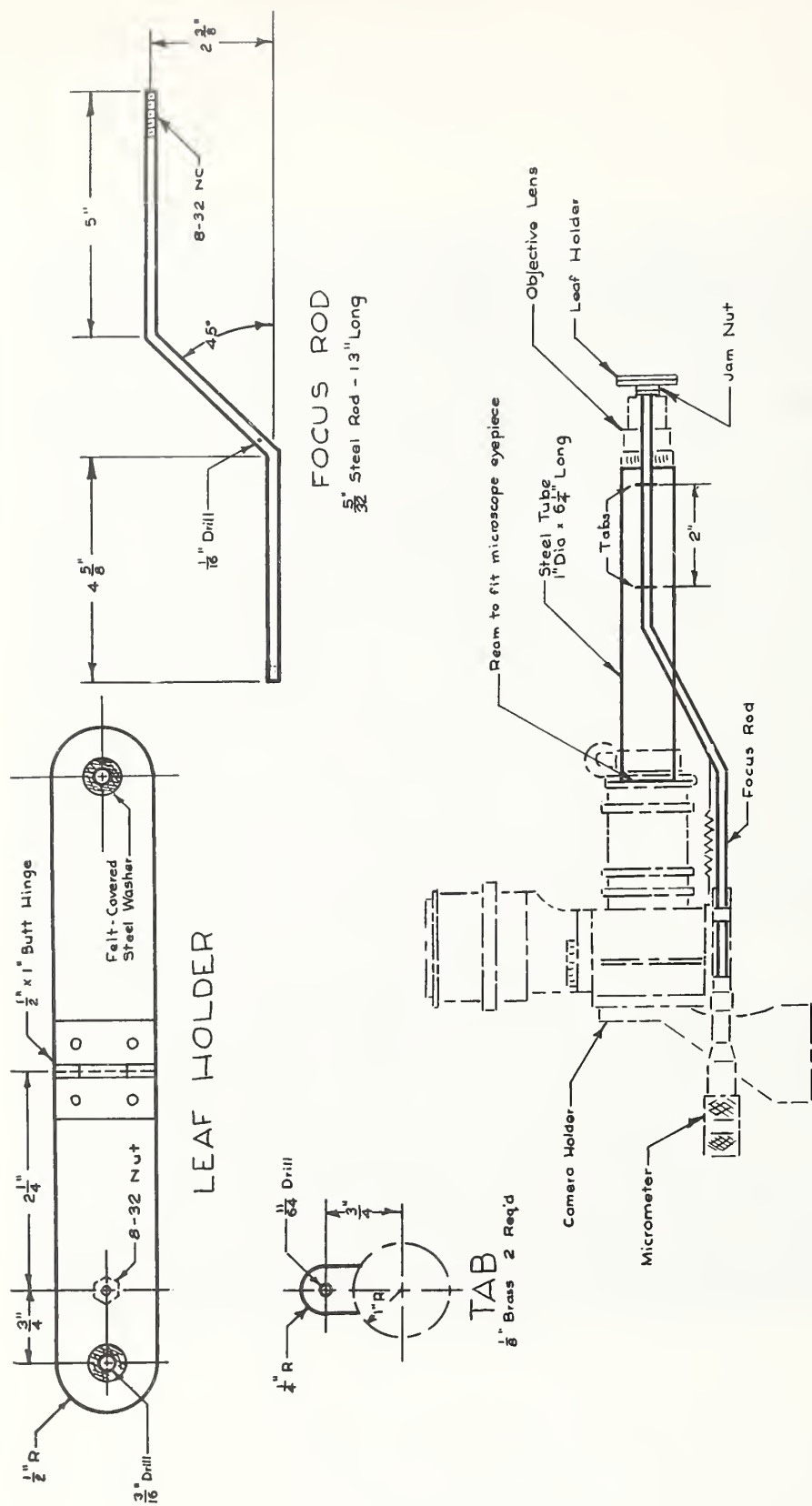


Figure 17. A detailed drawing showing the construction of the stomate camera.

of view, as well as good light-emitting qualities. Desired magnification was obtained by use of the 20X eyepiece. By means of an Ihagee adapter, the regular camera lens (Biotar 2/58) was mounted on top of the reflex viewer to give a 3X magnification of the image on the camera mirror to aid in focusing and observing.

The leaf holder was constructed of 20-gauge metal, so mounted as to permit movement to bring the object into focus. This is accomplished by means of a micrometer which was bolted to the bottom of the camera holder of the Ihagee Versal Unit. Velvet pads were placed inside the leaf holder to prevent damage to the leaf being photographed. The large holes in the leaf holder which can be seen in the photograph (fig. 16) were drilled to reduce the weight of the leaf holder.

In use, the leaf to be photographed is placed in the leaf holder and brought into focus by means of the micrometer. Light from a clear daylight sky or growth room light source is sufficient for focusing. To make a photograph the camera shutter is set on "bulb" position and held open while exposure is accomplished by an electronic flash directed through the leaf into the objective lens from a distance of about 6 inches. The low intensity flash from an Ascrolight Model A -423 electronic flash is sufficient for exposure of Kodak Plus-X Pan film. Figure 18 shows a photograph of plant stomates taken in the manner just described.

The same general procedure can be used for photographing leaves which are enclosed in leaf chambers. The leaf chamber itself will serve to hold the leaf in position and the photograph may be taken either through a transparent bottom in the leaf chamber or through a hole in the leaf chamber.

Possible disadvantages of the "stomate camera" might arise due to some adverse effect of placing the leaf in the leaf holder and the effect of the electronic flash on stomatal behavior. When a leaf is placed in the leaf holder, a small portion of the leaf is shaded and a very slight pressure is exerted on the leaf. The effects of these phenomena on stomatal behavior should be checked before using the camera on a particular species. With grain sorghum and red kidney bean plants there were no observable effects on stomatal opening due to placing the leaf in the leaf holder for the time required to make a photograph. A photograph can

1. The first part of the paper discusses the importance of the study of the history of the United States. It is argued that a knowledge of the past is essential for a full understanding of the present and for the development of a sound policy for the future. The author points out that the study of history is not merely a collection of facts and dates, but a process of critical thinking and analysis. It is through the study of history that we can learn from the mistakes of the past and avoid them in the future.

2. The second part of the paper discusses the role of the government in the development of the United States. It is argued that the government has played a crucial role in the development of the country, from the establishment of the Constitution to the present day. The author points out that the government has been responsible for the creation of the federal system, the establishment of the courts, and the development of the economy. It is through the government that we have been able to achieve the progress and prosperity that we enjoy today.

3. The third part of the paper discusses the role of the individual in the development of the United States. It is argued that the individual has played a crucial role in the development of the country, from the early settlers to the present day. The author points out that the individual has been responsible for the creation of the federal system, the establishment of the courts, and the development of the economy. It is through the individual that we have been able to achieve the progress and prosperity that we enjoy today.

4. The fourth part of the paper discusses the role of the future in the development of the United States. It is argued that the future is a time of great opportunity and challenge. The author points out that the future will be a time when we will have to deal with the problems of the present and the future. It is through the study of history that we can learn from the mistakes of the past and avoid them in the future.

5. The fifth part of the paper discusses the role of the future in the development of the United States. It is argued that the future is a time of great opportunity and challenge. The author points out that the future will be a time when we will have to deal with the problems of the present and the future. It is through the study of history that we can learn from the mistakes of the past and avoid them in the future.

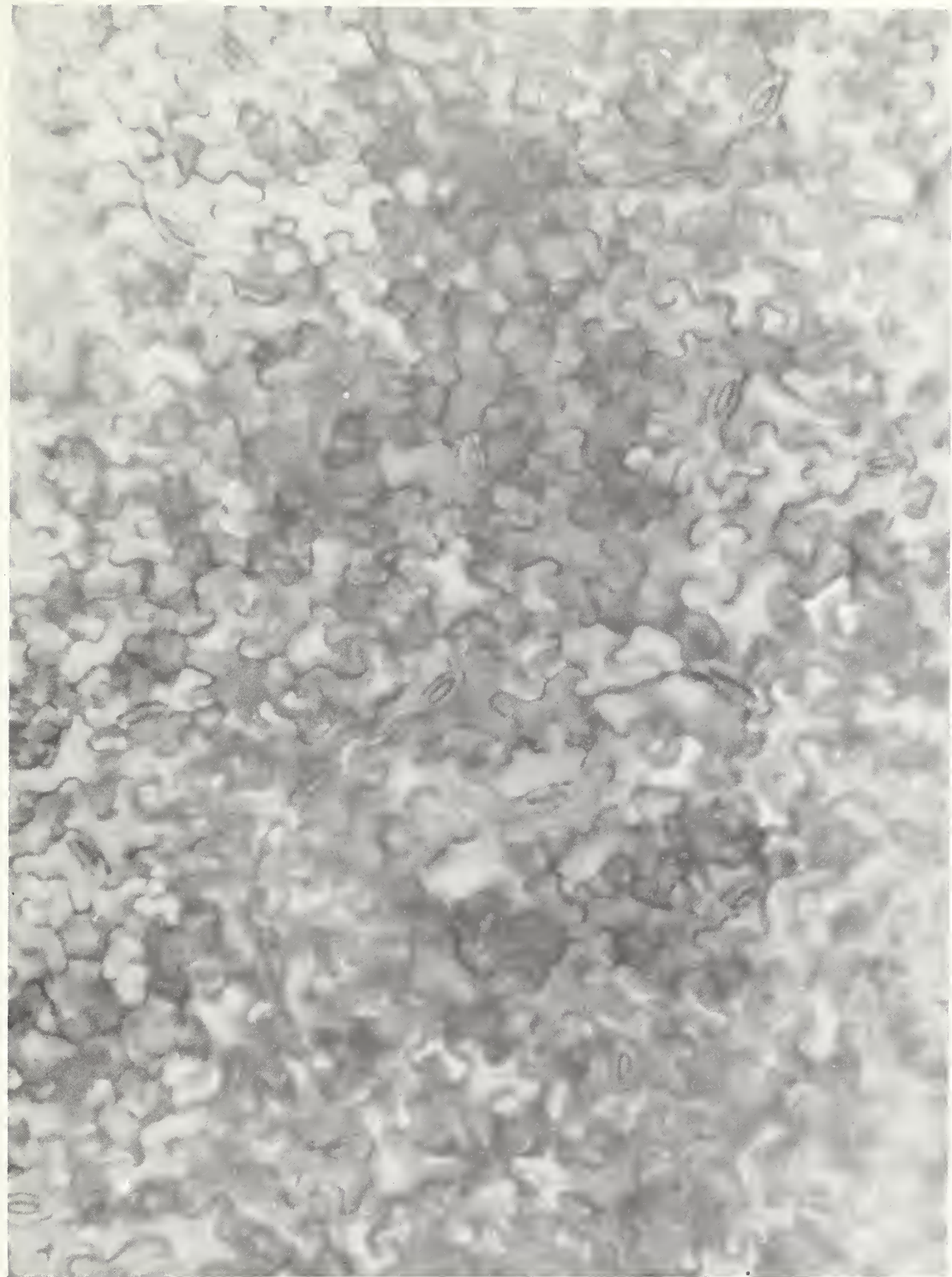


Figure 18. Open stomates of a red kidney bean plant.

usually be completed in 30 seconds to 1 minute after the leaf is placed in the holder. The electronic flash, of course, does not affect the stomatal opening recorded in the first photograph taken on a plant, but may have an effect insofar as subsequent photographs are concerned.

Testing has indicated that this camera should prove to be a useful tool for observing stomatal openings. The primary difficulty thus far has been getting sufficient areas of the field in focus for a good sample of stomates. With the Neofleur 6.3 objective, the depth of field is only 0.25 mm; therefore, with a rough leaf it is difficult to get a large area in focus. Little difficulty arises with smooth leaves.

The field of view with the 6.3 objective and 20X eyepiece is 0.50 x 0.75 mm. For routine printing of photographs the enlarger is set to give a final magnification of 550X. At this magnification, 1 mm on the picture is equal to 1.818 microns.

To obtain a quantitative evaluation of the stomatal openings, the perimeter of the opening is calculated by the formula for the perimeter of an ellipse, $P = a(4 + 1.1m + 1.2m^2)$ where $m = b/a$ and a and b are the major and minor axes, respectively. It is necessary to determine the perimeter of the stomatal opening rather than the area, diameter, or some other value since the diffusion of gases through small openings in a surface is dependent upon the perimeter of the openings.

CHAPTER III

SOLAR SPECTROPHOTOMETER

General Remarks.

One of the objectives of this project is to better understand the influence of light quality upon plant responses which may affect water utilization by plants. The wavelength bands that trigger stomate movement are of particular interest. In addition to determining the effect of light quality on plant responses, measurements will be made of the light absorption spectra of plants. The effect of different plant species, row spacings, leaf orientation and plant maturity upon light absorption patterns will be studied. The effect of leaf position on a plant on its energy absorption will be analyzed.

Spectrophotometer.

In order to undertake the light quality study it was necessary to design a spectrophotometer to measure direct radiation, transmitted radiation, reflected and scattered light from the plants. A spectroscopic instrument has been designed that is small, rugged, weatherproof, precise, sensitive, and capable of analyzing light from a large solid angle. The instrument had to be small and portable so that it could be placed among and beneath plants in their natural environment without disturbing the original plant geometry. It had to be rugged so that it could be transported without being damaged and so that it could be operated in any position. To permit operation under all types of climatic conditions, it was necessary to design a weatherproof system. This instrument is now under construction.

To simplify design, the present mode of operation will be from standard 115-volt, 60-cycle line current. The entire spectrometer system, including the data recording unit, is illustrated schematically in figure 19. The principal features of this system are the all sky lens, a double monochromator optical system, light-sensing element and related electronics, linear amplifier, strip-chart recorder, circular indicator, printing integrator, and position encoder and translator for triggering the printing integrator.

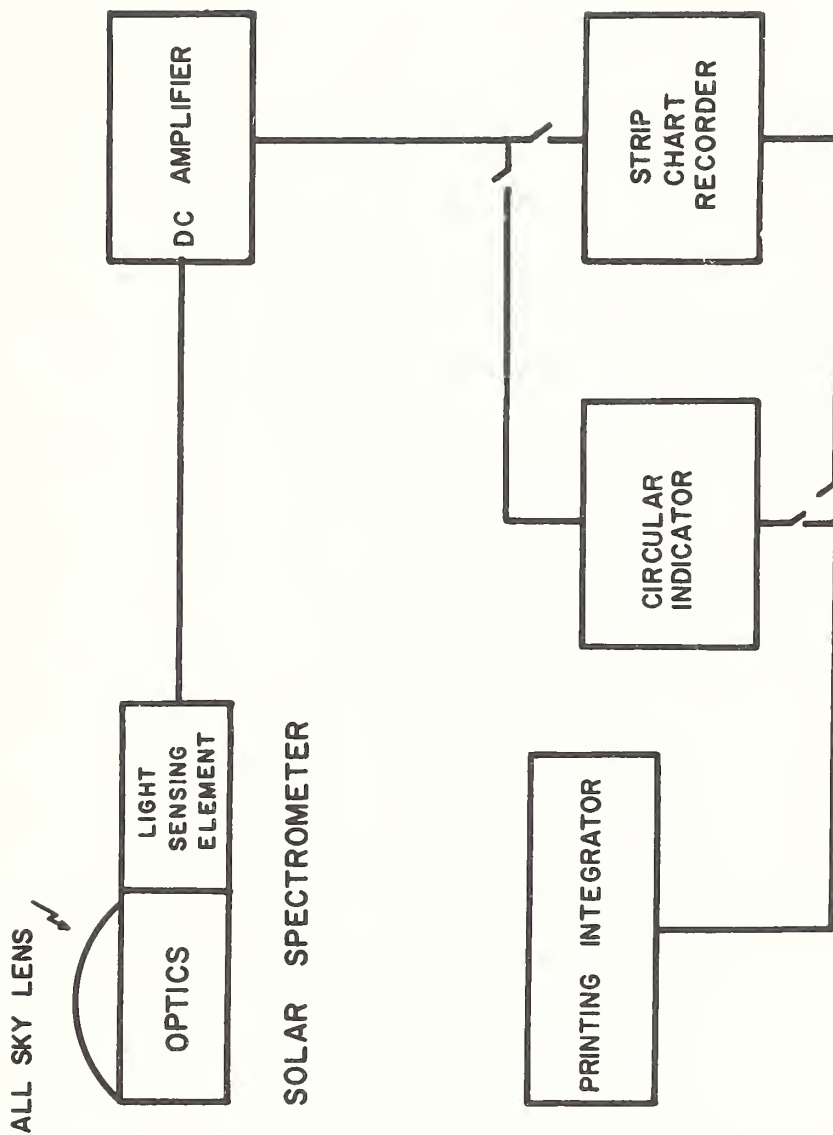


Figure 19. Solar Spectrophotometer.

All Sky Lens.

The all sky lens collects light from 180° or from all directions above a flat plane. This is an important feature because it permits the measurement of all light from all directions above a plane which is incident to a point. This means that direct, transmitted, reflected, and scattered light can all be measured simultaneously as one integrated amount. Other light collecting lenses can be used if it becomes desirable to measure directional radiation.

Double Monochromator.

The double monochromator optical system is a compact conventional assembly utilizing prisms, mirrors, and slits (fig. 20). In this system the radiations from 180° are brought to focus in a plane of 25.4 mm diameter by the all sky lens L_1 and then reflected through 90° by the mirror M_1 . This sky image is then reduced to 17 mm and focused by lens L_2 on the entrance slit S_1 . The light from S_1 is collimated by L_3 and then dispersed by the double monochromator which consists of the dense flint prisms P_1 and P_2 , and the mirrors M_2 and M_3 . All but the least deviated light is blocked from M_4 by the mechanical stop M.S. The light which is allowed to continue along the optical path is reflected by mirror M_5 and then modulated by the mechanical chopper C. The chopped light passes through the exit slit S_2 and is reflected through 90° by M_6 . Lens L_4 reduces the image to 2.5 mm and focuses it on the lead sulphide detector D_1 . D_1 produces an electrical signal that is proportional to the incident radiation.

The theoretical resolution for the optical system is less than 0.2 millimicrons for most of the spectrum and slightly higher in the infrared. The practical resolution, however, is that reached when the slits are set to pass the optimum amount of light. Optimum light will be that amount which drives the recording equipment to 95 percent of full range in the peak output region of the spectrum.

Electronic Circuitry.

The integrating spectrophotometer circuitry is illustrated in figure 21. The light will be modulated 150 times each second so that the sensing element will not fatigue. The signal caused by the light incident to the lead sulphide detector D_1 will be compen-

1. THE UNITED STATES OF AMERICA
 2. DO HEREBY DECLARE THAT
 3. IT IS THE POLICY OF THE UNITED STATES
 4. OF AMERICA TO OPPOSE ANY ATTEMPT TO
 5. OBSTRUCT OR IMPEDIMENT TO THE LIBERTY
 6. OF TRAVEL AND COMMERCE ACROSS THE INTERNATIONAL
 7. BOUNDARIES OF THE UNITED STATES OF AMERICA
 8. AND TO OPPOSE ANY ATTEMPT TO OBSTRUCT OR IMPEDIMENT TO THE LIBERTY OF TRAVEL AND COMMERCE ACROSS THE INTERNATIONAL BOUNDARIES OF THE UNITED STATES OF AMERICA

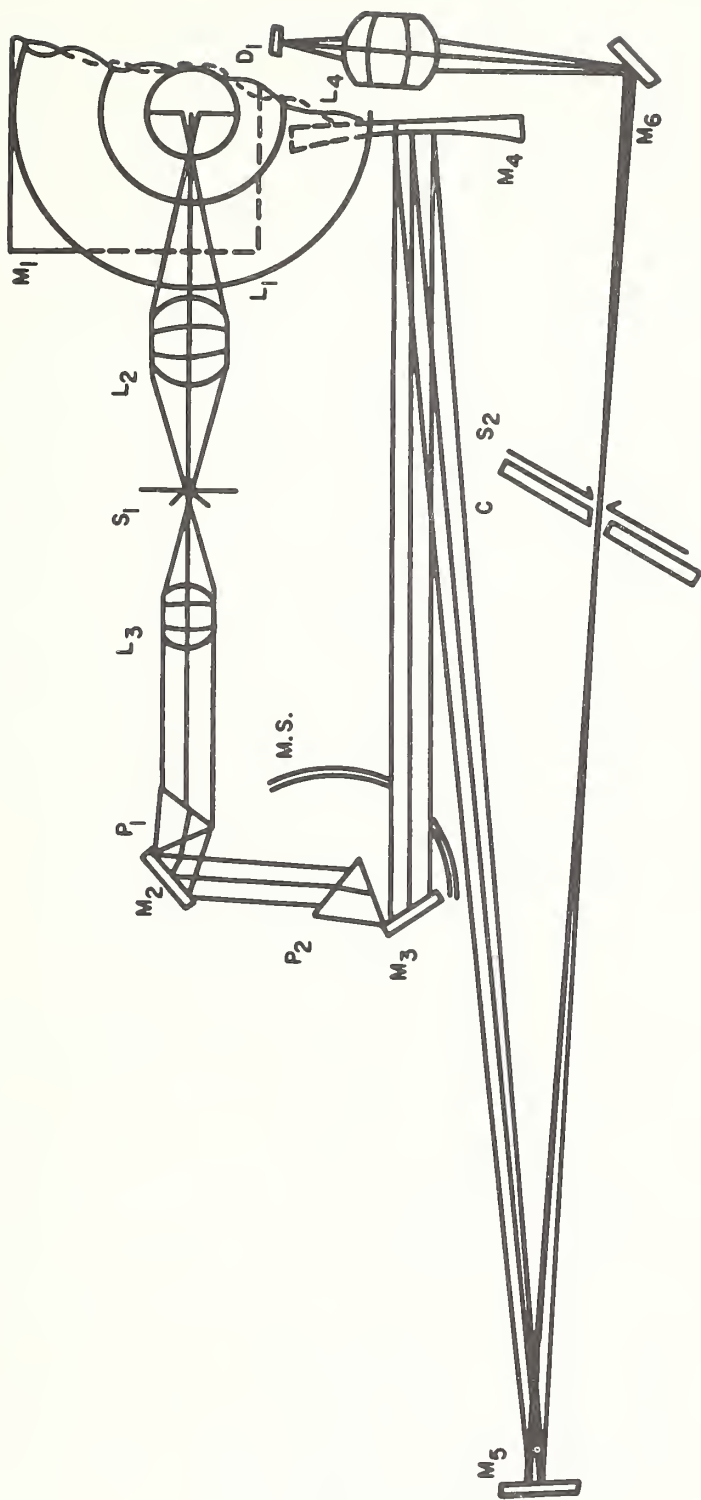


Figure 20. Integrating spectrophotometer optics.

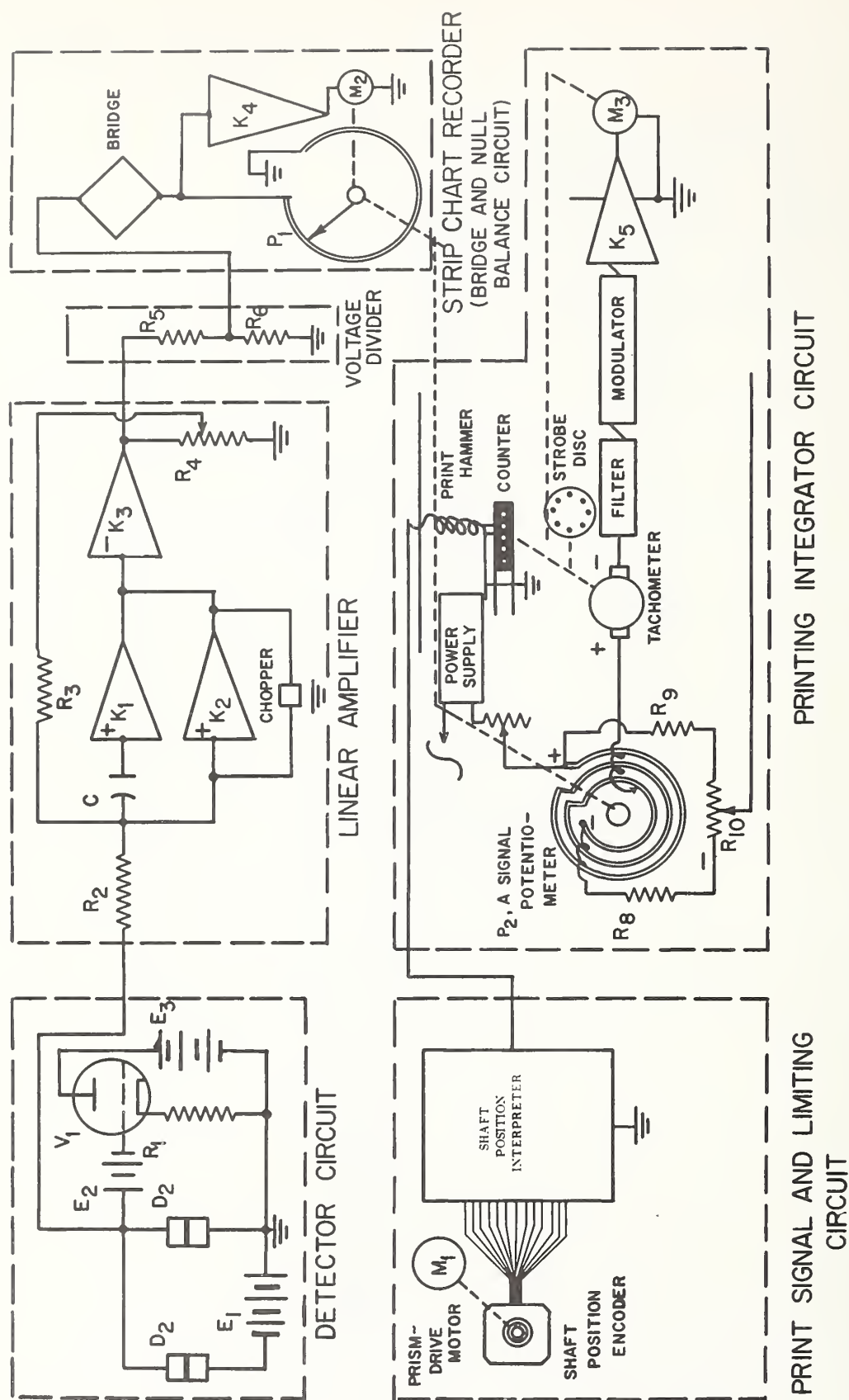


Figure 21. Integrating spectrophotometer circuitry.

sated for temperature effects by a shielded detector D_2 that is matched for response against D_1 . This signal will be amplified in the detector circuit. Necessary voltages will be supplied to the detector circuit through E_1 , E_2 , and E_3 . The preamp tube V_1 is chosen to correct for nonlinearity in response to light intensity. The signal from V_1 will be fed into the input of the linear amplifier.

The first stage of the linear amplifier consists of a wide band audio amplifier K_1 and a chopper stabilized D.C. amplifier K_2 . The signals from K_1 and K_2 are summed and fed to a wide band amplifier K_3 , which acts on all frequencies. Part of the signal from K_3 is tapped off by precision resistances R_4 from inverse feedback. This feedback can be selected to give 10 precise gains of from 0 to 1,000. The amplified signal will be connected to the strip chart recorder or circular indicator.

If the strip chart recorder is used in the system, then a permanent pen trace of the solar spectrum will be obtained for each sweep. This will be desirable for initial and periodic checking out of the system but will be of little benefit during routine operations. To quantitatively evaluate the results by integrating the area under the curve of strip charts would be too laborious and would seriously limit the amount of data that could be collected and processed. For most runs, the circular indicator will be used to monitor the signal strength and drive the printing integrator. The strip chart recorder has also been modified so that it will drive a printing integrator while simultaneously drawing a pen trace.

The printing integrator utilizes a standard velocity-servo computing arrangement with the input signal produced by a potentiometer installed on the recorder shaft. Within the integrator an amplifier drives a servo-motor, rigidly coupled to a tachometer generator and to a printing counter that registers the total number of shaft turns accumulated. The tachometer generator produces an output voltage that is linearly proportional to the speed at which it is driven by the servo-motor. The amplifier compares the signal produced by the tachometer to that from the potentiometer installed in the recorder (or circular indicator) and continuously regulates the speed of the servo-motor and tachometer to balance exactly the potentiometer signal with the tachometer voltage. Thus each value of the potentiometer input corresponds to a definite servo-motor and tachometer speed. Since the printing counter's rate of rotation

is proportional to the recorder pen position, the total number of turns registered in a given time interval is proportional to the integral of the recorder pen position during the same time interval, and therefore, is proportional to the area under the curve drawn by the pen. A maximum integrating rate of 6,000 counts per minute is possible.

The integrated energy accumulated within each of the spectral regions under investigation will be proportional to the difference in the printed counts at the beginning and ending of the period. Average intensity for each region will be equal to total energy absorbed, divided by the time required to sweep the region. Once the regions have been selected, IBM computer programs will be developed so that all calculations can be made using only the data printed by the integrator. This will speed calculations and put the resulting data onto cards for statistical analyses.

The integrator will be triggered at the start of each spectral region by an encoder-translator system which is connected to the rotating prism table in the spectrophotometer. The encoder has been geared to give a resolving power of 1 part in 4,000 for the complete sweep of the spectrum. The translator output can be programmed to trigger the integrator at any one of these positions. This capability permits the selection of regions of different widths. It will therefore be possible to mix narrow wavelength bands of special interest and broad bands of general interest. This feature increases the flexibility and adaptability of the system to the different research projects which will utilize the spectrophotometer system.

Research Investigations.

The light quality study will be divided into a growth room phase and a field phase. The incandescent light sources of the growth room will be analyzed for spectral energy emissions as influenced by line voltage and depth of water in the filters used to dissipate heat from the bulbs. Colored cellophane films and chemical additives in the water filters may also be studied.

After reproducible physical conditions are obtained, plants will be subjected to light sources of varying quality. The influence of the different spectral distributions will be carefully observed.

Field studies of light absorption by plants will be conducted on plots of corn, sorghum, soybeans, small grains, Bermuda grass, and cotton. The effect of row spacings, row direction, distance between the plants in a row, and leaf position on the plants will be analyzed as to effect upon light-quality absorption.

CHAPTER IV

GUARD CELL ACTION

General Remarks.

In recent years increasing emphasis has been given to the importance of accumulating transpiration data under certain controlled environmental conditions. The usefulness of this information, however, has been limited by the lack of comprehension of the complex processes operating on the cellular level. Although much literature is available on stomatal physiology, the mechanism or mechanisms responsible for guard cell operation are not understood. A thorough search of the literature was conducted to obtain background information: the references are included in the bibliographic supplement I to this report.

Mechanism of Guard Cell Action.

The commonly accepted theory of the operation of guard cells depends upon a starch to sugar equilibrium existing in the guard cells. The preponderance of evidence substantiates this. The actual movement observed in the opening and closing of the stomata is considered the end result of a change in turgor pressure in the guard cells. By the conversion of starch to sugar, there is a concomitant increase in the osmotic pressure, resulting in a change of turgor pressure. The equilibrium position of starch to sugar conversion seems to be pH sensitive, lying on the starch side at low pH values and on the sugar side at higher pH. Probably the pH changes normally in the guard cells as a result of photosynthesis and respiration. For instance, in the dark, CO_2 produced by respiration and dissolved in the cell sap and cytoplasm would keep the cell reaction acid; however, under conditions where photosynthesis takes place, CO_2 would be utilized and thus shift the pH of the cell toward alkalinity. Evidently the pH changes are not of any great magnitude and probably do not exceed more than 2 units under extreme conditions.

If this relatively simple explanation of guard cell mechanism is true, it would seem that opening and closing of guard cells could be induced by modifying the environment of the cell. Virgin (13) and Shaw (10) have both reported they were unable to open the stomata of albino barley plants.

Their experiments were not reported in detail. It is still necessary to determine whether experimental conditions can be imposed on albino plants to cause their stomata to open or close. Experiments of this kind could yield information pertinent to our problem. Therefore, efforts were made to obtain albino plants. Seed reported to produce albino plants was obtained from many geneticists and seed houses. Seedlings of tobacco, sorghum, soybeans, cotton, oats, millet, and corn were grown but to date only the corn has given a true albino or truly white plant. Albino corn, both yellow and white, made measurable growth when cultured on .3M sucrose (fig. 22) as described by Spoehr (12). It was this corn that provided test material in limited quantity for the following preliminary experiments. Periodic observations by use of the microscope showed most stomata did not open under the leaf feeding technique, although about 1 in 100 did.

Scarath (8) early reported that acetic acid vapor would close and ammonium hydroxide vapor would open stomata. These vapors were tried several times under different conditions, but had no effect on the stomatal opening of albino corn leaves. A more direct method was then employed by changing the pH of the .3M sucrose solution. A carbonate buffer series was used to obtain pH values of 5.8, 6.8, and 7.8. These treatments had no apparent influence on stomatal opening during a 48-hour period of observation.

Microscopic examination of the guard cells from yellow and white corn leaf tissue showed considerably fewer plastids in the paper white cells. This is probably a reflection of the decrease in plastic number reported to exist in albino tissue (Schwartz, 9). IKI stain failed to show any starch accumulation. The failure of the cells to respond could be due to the lack of sucrose penetration. To increase the effectiveness of sucrose penetration into the cells, two surface active agents, Nonic 218 and Tween 20, were added to the sucrose solution. Nonic 218 had no effect on stomatal opening, but the Tween 20 addition caused the opening of as many as two-thirds of the stomata in that portion of leaf actually immersed in the solution (fig. 23). However, lysis of cells near the open stomata was commonly observed (fig. 24). Further work with albinos has been curtailed until more knowledge of the pathway of starch accumulation and degradation in guard cells has been accumulated.



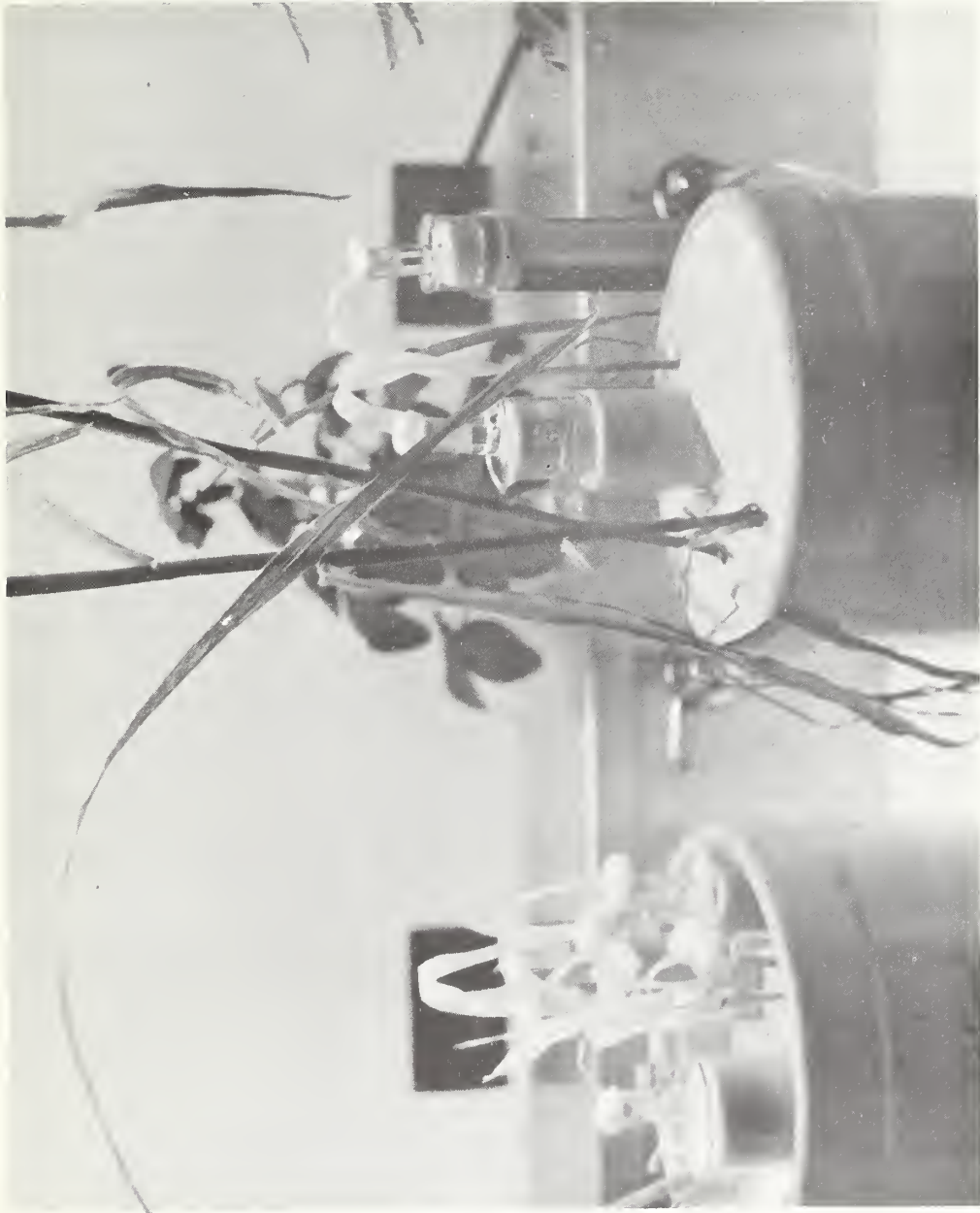


Figure 22. Albino corn seedlings fed by periodically cutting leaves and immersing in .3 M sucrose.

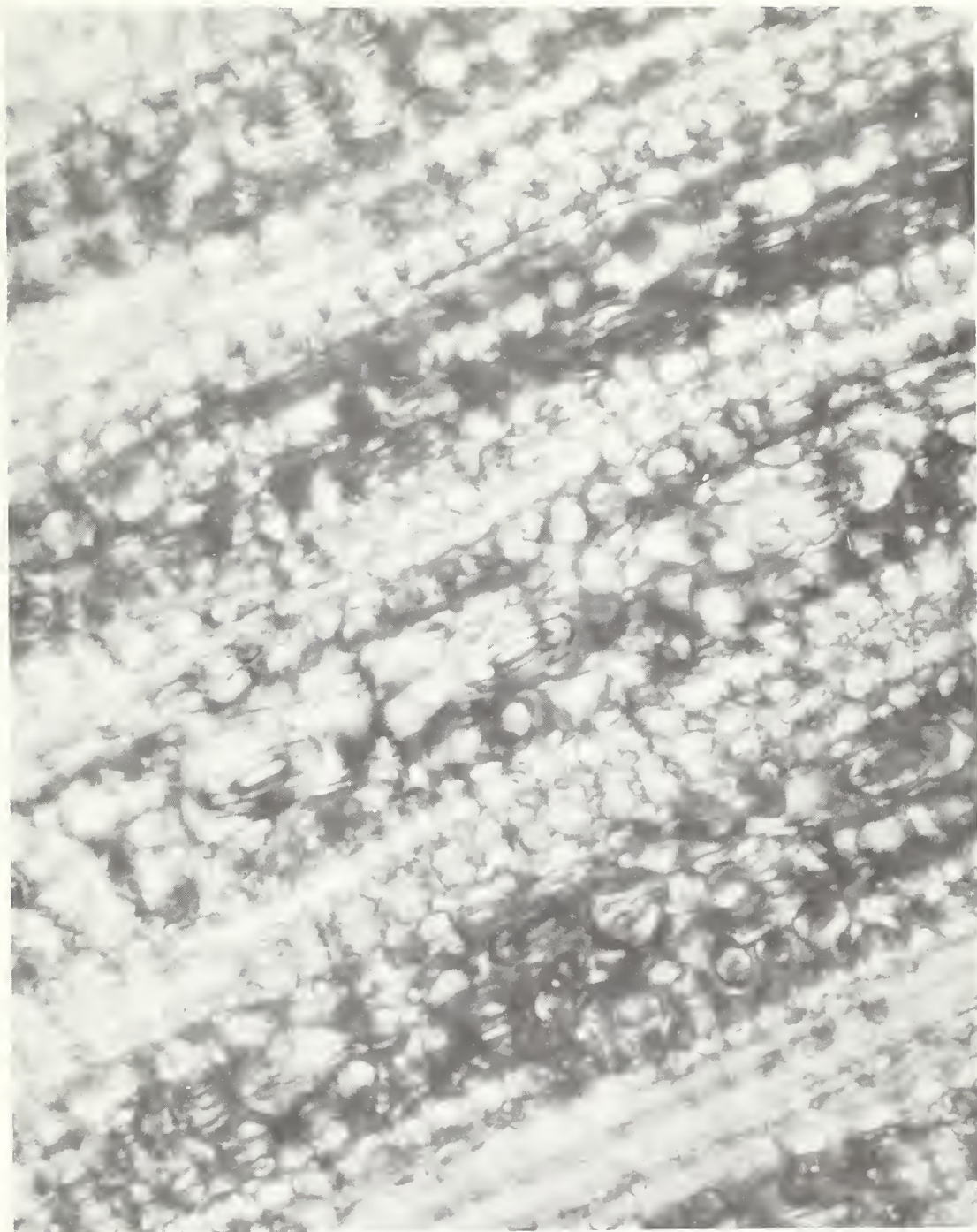


Figure 23. Albino guard cells opened by Tween 20 and sucrose treatment.



Figure 24. Typical lysis of cells in area of Tween 20 and sucrose treatment.

There is very good evidence that photosynthetic products produced in the guard cells, especially in guard cells showing a paucity of chlorophyll, cannot account for the large amount of stored starch normally found in guard cells. Guard cells must have the capacity to accumulate sugars produced in chlorenchyma cells; in fact, preliminary experiments have confirmed this capacity of the guard cells. Guard cells of corn and bean seedlings grown in the dark accumulate starch from stored carbohydrates in the seed. Small amounts of this starch are retained even though the plants eventually die due to lack of carbohydrates. Senescent bean leaves were also found to contain starch in guard cells after abscission. Lloyd (7) postulated that guard cells derive their starch chiefly from the underlying tissues rather than through their own photosynthetic activity. Further preliminary experimentation has shown that Lloyd's hypothesis is probably correct. Etiolated leaves of corn and beans accumulated large quantities of starch in their guard cells when partially immersed in .3M sucrose solution. A preferential accumulation of starch occurred in the guard cells most proximal to the sucrose feeding.

The question arose as to whether the ability for starch accumulation in guard cells from the externally applied sucrose was completely dependent on chlorenchyma cells. Epidermal peelings of corn and bean leaves were compared with leaf sections in .3M sucrose solutions for their capacity to store starch in the guard cells. The guard cells in the peelings accumulated as much starch as the leaf sections in 24 and 48 hours, demonstrating their inherent ability to convert sucrose. This also indicates the sugar may translocate to the epidermis as sucrose. Figure 25 shows starch stored in bean guard cells after supplementary feeding.

Other species, representatives of Angiospermeae, will be similarly checked for starch synthesis with a view of establishing a possible biochemical pathway of starch production in guard cells.

Control of Guard Cell Action.

Since one of the ultimate objectives of this task is to control transpiration, some efforts were directed toward the use of two growth regulators reported to have an effect on guard cell operation; namely, 2,4-dichlorophenoxyacetic acid (2,4-D) and B-naphthoxyacetic acid. Red kidney bean plants

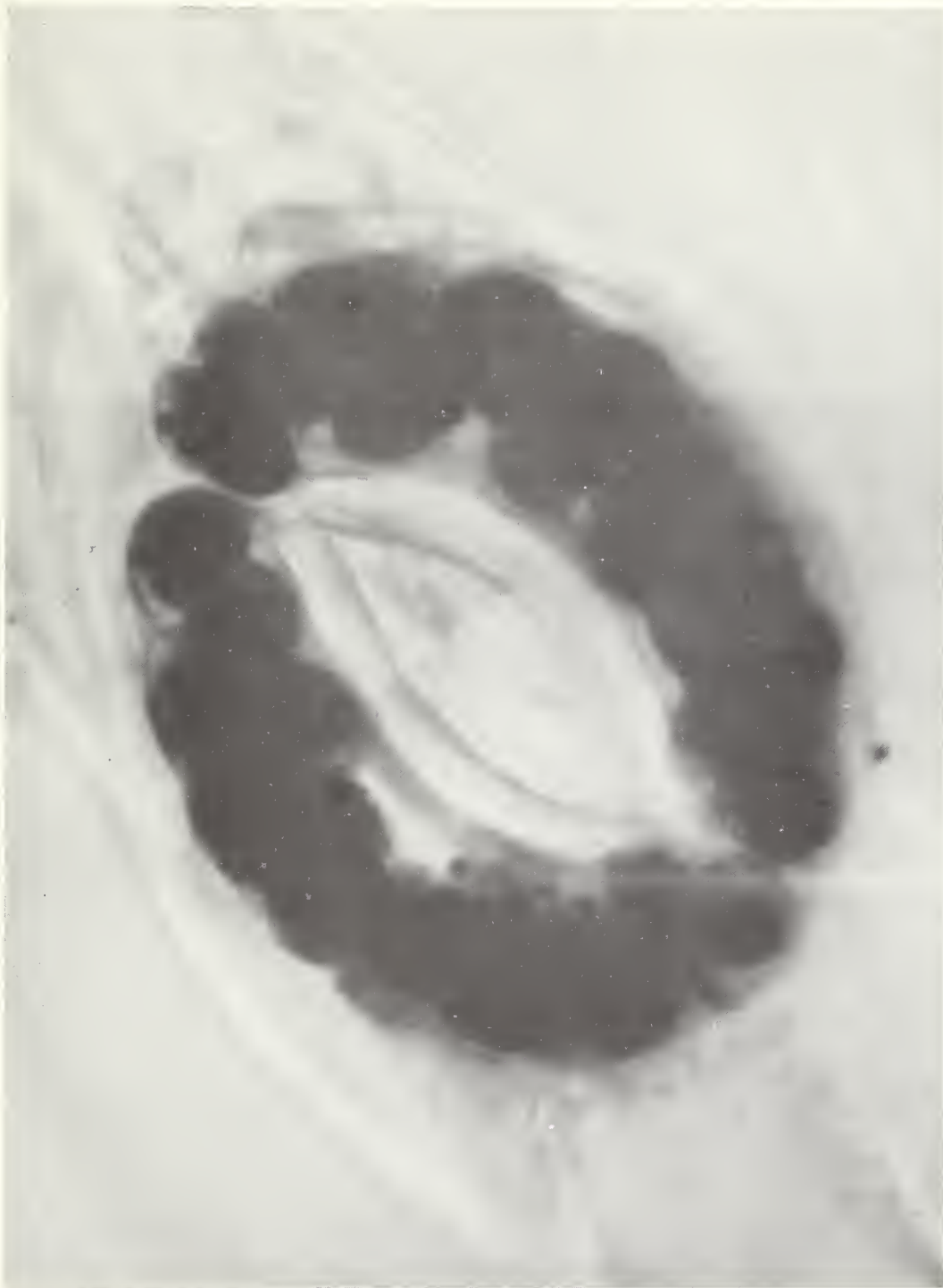


Figure 25. Stoma of etiolated bean plant; dark objects in each guard cell are starch grains derived from sucrose feeding.

were grown in Hoagland's solution in controlled chambers until at least one group of trifoliate leaves on each plant was fully expanded. The plants were sprayed until runoff with aqueous solutions containing 625, 125, 25, 5, and 0 ppm of 2,4-D or B-naphthoxyacetic acid as the triethylamine salt, with .05 percent Vatsol OT as a surface active agent. Water loss was measured daily prior to spraying and after spraying. Figure 26 shows that up to the day of spraying, water loss was relatively uniform, but after spraying, the higher the concentration of 2,4-D sprayed, the greater the decrease in transpiration. The highest concentration of 2,4-D eventually killed the plants; the final dry weight of all plants was inversely related to the treatment concentration. Its effect on the transpiration of a monocot remains to be studied.

Because of a malfunctioning control unit, plants in the B-naphthoxyacetic acid experiment were subjected to freezing temperatures the second night after spraying. This resulted in termination of the experiment at an early stage. However, it is obvious that transpiration was considerably reduced at the high concentration of B-naphthoxyacetic acid. Whether deleterious effects would have been observed is not known at this time. (See fig. 27.)

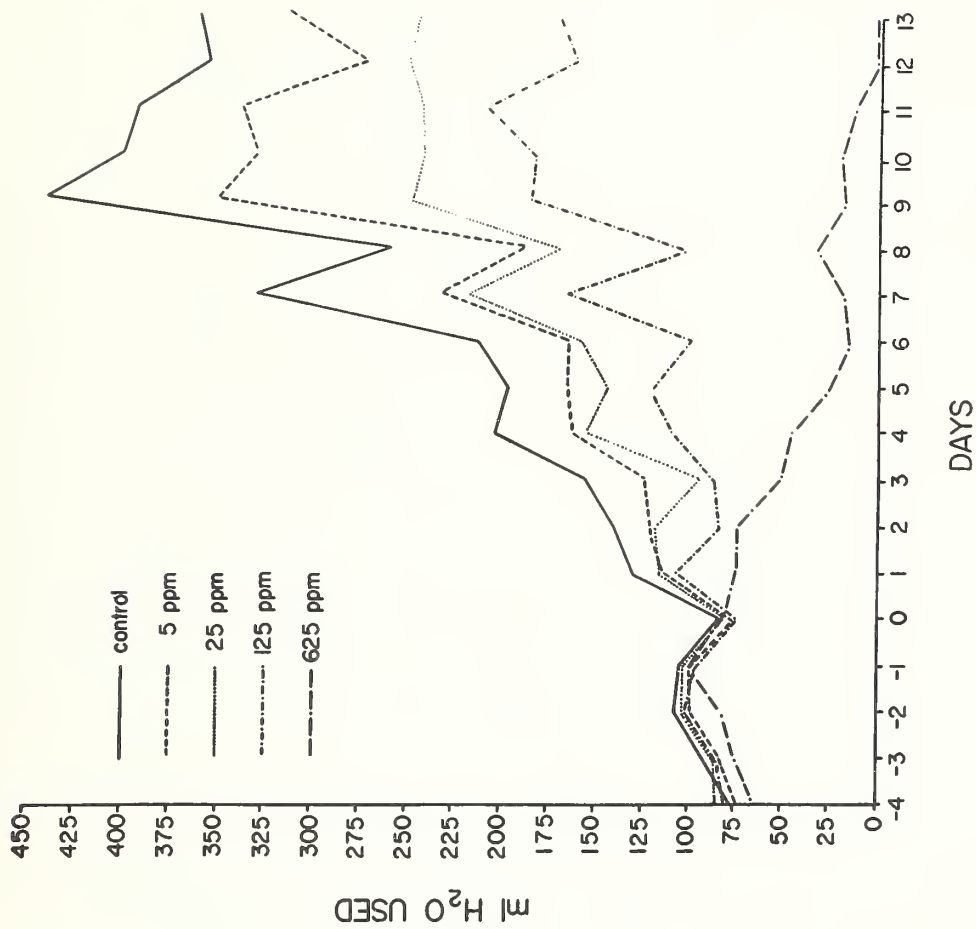


Figure 26. Transpiration loss of red kidney bean plants treated at indicated concentrations with 2,4-dichlorophenoxyacetic acid.

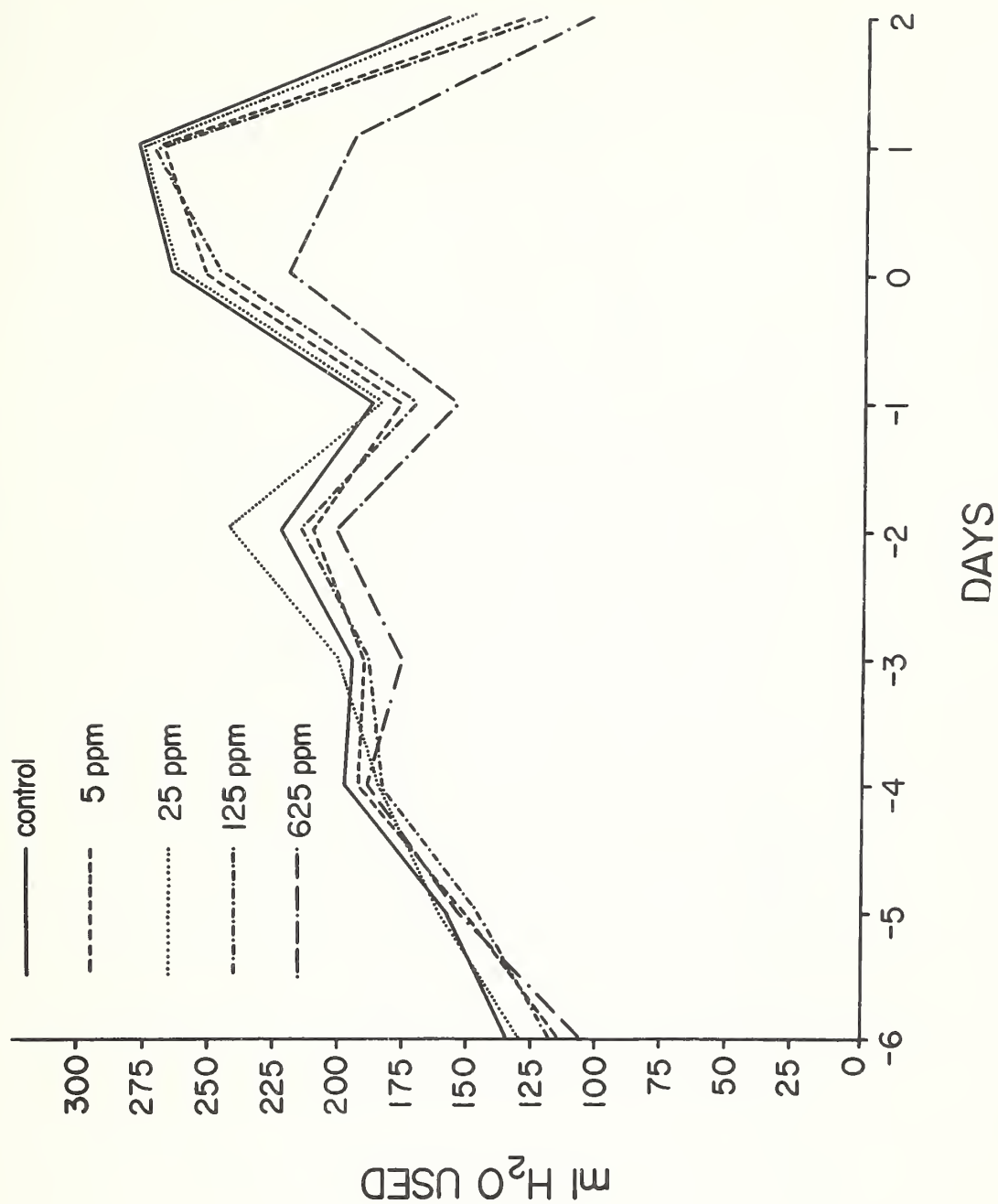


Figure 27. Transpiration loss of red kidney bean plants treated at indicated concentrations with β -naphthoxyacetic acid.

LITERATURE CITED

1. Alvim, P. de T., and J. R. Havis. An improved infiltration series for studying stomatal opening as illustrated with coffee. *Plant Physiol.* 29:97-98. 1954
2. Anderson, N. E., C. H. Hertz, and H. Rufelt. A new fast recording hygrometer for plant transpiration measurements. *Physiol. Plantarum.* 7:753-767. 1954
3. Darwin, F., and F. F. M. Pertz. On a new method of estimating the aperture of stomata. *Proc. Roy. Soc. London B.* 84:136-154. 1911
4. Heath, O. V. S. Studies in stomatal behavior. V. The role of carbon dioxide in the light response of stomata. Part I. Investigation of the cause of abnormally wide stomatal openings within porometer cups. *Jour. Exptl. Bot.* 1:29-62. 1950
5. Knight, R. C. A convenient modification of the porometer. *New Phytologist.* 14:212-216. 1915
6. Livingston, B. E., and E. B. Shreve. Improvements in the method for determining the transpiring power of plant surfaces by hygrometric paper. *Plant World.* 19:287-309. 1916
7. Lloyd, F. E. The physiology of stomata. *Carnegie Inst. Wash. Pub.* 82:1-142. 1908
8. Scarth, G. W. Mechanism of the action of light and other factors on stomatal movement. *Plant Physiol.* 7:481-504. 1932
9. Schwartz, D. The chlorophyll mutants of maize. *Botan Gaz.* 111:123-130. 1950

1. The first part of the paper is devoted to a general discussion of the problem of the existence of solutions of the system of equations (1) and (2) for arbitrary values of the parameters α and β .

2. In the second part, we consider the case when the parameters α and β are chosen such that the system of equations (1) and (2) has a unique solution. This case is of great interest for applications.

3. In the third part, we study the properties of the solutions of the system of equations (1) and (2) for arbitrary values of the parameters α and β . We show that the solutions are unique and stable with respect to the initial conditions.

4. In the fourth part, we consider the case when the parameters α and β are chosen such that the system of equations (1) and (2) has a unique solution. This case is of great interest for applications. We show that the solutions are unique and stable with respect to the initial conditions.

5. In the fifth part, we study the properties of the solutions of the system of equations (1) and (2) for arbitrary values of the parameters α and β . We show that the solutions are unique and stable with respect to the initial conditions.

6. In the sixth part, we consider the case when the parameters α and β are chosen such that the system of equations (1) and (2) has a unique solution. This case is of great interest for applications. We show that the solutions are unique and stable with respect to the initial conditions.

7. In the seventh part, we study the properties of the solutions of the system of equations (1) and (2) for arbitrary values of the parameters α and β . We show that the solutions are unique and stable with respect to the initial conditions.

8. In the eighth part, we consider the case when the parameters α and β are chosen such that the system of equations (1) and (2) has a unique solution. This case is of great interest for applications. We show that the solutions are unique and stable with respect to the initial conditions.

9. In the ninth part, we study the properties of the solutions of the system of equations (1) and (2) for arbitrary values of the parameters α and β . We show that the solutions are unique and stable with respect to the initial conditions.

10. Shaw, M. The physiology of stomata. II. The apparent absence of chlorophyll, photosynthesis, and a normal response to light in the stomatal cells of an albino barley. *Can. Jour. Bot.* 36:575-579. 1958
11. Spanner, D. C. On a new method for measuring the stomatal aperture of leaves. *Jour. Exptl. Bot.* 4:283-295. 1953
12. Spoehr, H. A. The culture of albino maize. *Plant Physiol.* 17:397-410. 1942
13. Virgin, H. I. Stomatal transpiration of some variegated plants and chlorophyll-deficient mutants of barley. *Physiol. Plantarum.* 10:170-186. 1957
14. _____. Light-induced stomatal movements in wheat leaves recorded as transpiration. Experiments with the coronahygrometer. *Physiol. Plantarum.* 9:280-303. 1956
15. Williams, W. T. Studies in stomatal behaviour. III. The sensitivity of stomata to mechanical shock. *Annals of Bot. N. S.* 13:309-327. 1949

